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Adaption of the Potato to Hot-Dry Climates

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TABLE OF CONTENTS

	Page
A. REPORT	3
A.1. Physiological Studies of Heat Tolerant Potato Clones.....	3
A.1.1. Abstract	4
A.1.2. Introduction.....	5
A.1.3. Materials and Methods.....	6
A.1.4. Results	10
A.1.5. Discussion	12
A.1.6. References.....	16
A.2. Variations in Patterns of Osmotic and Proline Concentration and Their Association with Dry Matter Production and Partitioning in Potatoes (<i>Solanum tuberosum</i> L.) Exposed to Transient Heat and Drought Stress	27
A.2.1. Abstract	28
A.2.2. Introduction.....	29
A.2.3. Materials and Methods.....	31
A.2.4. Results	33
A.2.5. Discussion	35
A.2.6. References.....	40
B. EVALUATION OF THE RESEARCH ACHIEVEMENT WITH RESPECT TO THE ORIGINAL RESEARCH PROPOSAL.....	56
C. DESCRIPTION AND RESULTS OF COOPERATION	57
D. LIST OF THESES	58
(Full text of each thesis attached)	

PHYSIOLOGICAL STUDIES OF HEAT TOLERANT POTATO CLONES

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Abstract

Sufficient genetic diversity exists within the cultivated potato (*Solanum tuberosum* L.) so that selection of heat tolerant genotypes is possible. However, selection based on productivity at high temperature is impractical for large populations, and results may vary with locations and years. Identification of physiological traits that are associated with heat tolerance would enhance the selection procedure. The relationship between photosynthesis, respiration, partitioning of ^{14}C labeled assimilates and productivity of potato clones with a range of heat tolerance was studied. Uniform single stem plants of seven clones (Desiree, DTO-28, Katahdin, Kennebec, LT-1, DNA1725-1, and Russet Burbank) were grown in greenhouse and growth chambers at low (20-25°C day/12-15°C night) and high (32-38°C/25-28°C) temperatures and 12 to 15 hour photoperiod. Total dry matter production and growth rates were determined after 2 to 5 weeks growth at each temperature. Photosynthesis and dark respiration rates of leaves were measured on several dates by infrared gas analyzer and radioisotope techniques. Partitioning patterns of ^{14}C assimilates were followed after labeling the most recently expanded leaf with $^{14}\text{CO}_2$ for 30 minutes. Two heat tolerant clones (DTO-28 and NDA1725-1) consistently produced the highest dry matter, and had the fastest rates of growth at both temperatures. Dry matter production was negatively correlated with dark respiration rate, but unrelated to photosynthesis rates in the clones studied. Both DTO-28 and NDA1725-1 tended to have lower ratios of respiration/photosynthesis than other clones. High temperatures altered dry matter distribution and partitioning of ^{14}C assimilates in favor of vines at the expense of tubers. Translocation of ^{14}C assimilates out of labeled leaves was reduced at high temperatures. Clones that partitioned the greatest portion of carbon to tubers at high temperature did not necessarily produce the highest harvestable yields. The differences in photosynthesis and dark respiration rates among these clones, and their relationship to plant productivity indicates a usefulness for these traits in selection of high yielding cultivars. It may be possible to combine (through

breeding or other methods) high rates of photosynthesis, low respiration, and ability to partition a high portion of carbon to tubers, thus enhancing productivity under all environments.

Introduction

The potato is a cool season crop conventionally grown in areas of northern latitudes and higher elevations where temperatures are mild during part of the year. Heat stress is an important constraint that limits the expansion of this crop to hotter regions in the world. Because of limitations imposed by high temperature on dry matter accumulation and distribution, there has been a major effort to select potato germplasm with heat tolerance (20). Field screening techniques have been developed for use in identifying clones with high levels of heat tolerance (16,17,29). However, evaluation of large populations for heat tolerance based on yield characteristics is very time consuming (22,27). Identification of physiological traits associated with heat tolerance would greatly enhance the ability to select parents and screen subsequent progeny (20,22,27,28).

Three physiological processes have major impact on potato crop productivity under hot conditions: (1) the ability to maintain high levels of carbon fixation by leaves, (2) the ability to minimize respiratory losses and (3) the ability to partition a high proportion of carbon assimilates to the tubers. Crop adaptation to abnormal conditions is determined by the range of variability that exists in germplasm and the ability of plants to acclimate to environmental extremes. Genotypes able to tolerate heat stress may have higher photosynthesis (4,19,25) or lower respiration (25,32) at high temperatures than genotypes adapted to cool climates. Wivutvongvana (33) found that heat tolerant clones of *Solanum acuale* and *chacoense* had lower leaf dark respiration rates than sensitive clones, but similar photosynthesis rates. Cultivated potatoes (*Solanum*

tuberosum) exhibit consistent variation in both photosynthesis (8,21) and respiration (18), but these differences have not been related to heat tolerance. If tuber production is source limited at high temperatures, then increasing the production of assimilates, by increasing photosynthesis or reducing respiration, should increase yields (1).

Distribution of ^{14}C labeled assimilate within potato plants is related to pattern of dry matter distribution during the season (11). Genetic, environmental and nutritional influences on dry matter partitioning result in changes in pattern of ^{14}C photoassimilate partitioning (11,12,23,24,26). Differences in tomato cultivar tolerance to heat stress have been explained based on ^{14}C translocation and partitioning (6,7). The value of ^{14}C partitioning patterns as physiological indicators of relative heat tolerance in potato has not been reported.

The objective of this study was to determine if potato clones exhibit differences in photosynthesis, respiration and ^{14}C carbon partitioning that are related to heat tolerance.

Materials and Methods

A series of experiments was conducted between 1986 and 1989. Because the results were mostly similar, only the most illustrative data are presented.

Photosynthesis and Respiration Studies

Six potato clones were selected for study: Desiree, DTO-28, Katahdin, Kennebec, NDA1725-1, and Russet Burbank. Seed pieces were planted in flats containing a sand, vermiculite and peat moss soil mixture (2:2:1 by volume). Plants were grown at low greenhouse air temperatures (25°C day/ 12°C night $\pm 3^{\circ}\text{C}$) for 28 days, then the most uniform plants were transplanted to 6.6 liter pots containing the same sand, vermiculite and peat moss soil mixture. At transplanting each plant received 100 ml of 20N/8.7P/16.6K soluble fertilizer solution (400 ppm N). Plants were fertilized based on petiole nutrient concentration for the remainder of the experiments. Plants were watered

to run off twice daily to avoid water stress. Greenhouse temperatures were maintained at 25°C day/12°C night up to the start of the temperature treatments.

Soil and air temperature treatments were begun approximately two weeks after plants initiated tubers (58 days after planting). Eight uniform plants of each clone were harvested, and all plant organs, including vines, tubers, roots and stolons, were dried at 70°C for three days before being weighed. Another eight plants of each clone (including pot and soil) were placed in boxes, and moist sand packed around the pots. Soil temperatures were maintained at $16 \pm 2^\circ\text{C}$ in half of the plants, the other half were at $30 \pm 2^\circ\text{C}$ (measured at 10 cm depth). Plants were arranged in a randomized complete block design with four replications within each soil temperature regime. Soil temperatures were kept constant by a thermostatically controlled system that circulated water through copper tubing placed next to the pots. The surface between pots was covered with styrofoam insulation to reduce temperature fluctuations.

In the first part of the experiment air temperatures remained at 25°C day/12°C night for the rest of the growth period. In the second part, air temperatures were increased to 38°C day/28°C night $\pm 4^\circ\text{C}$ (high temperature) after plants were placed in boxes. Because plants in the low and high air temperature greenhouses were grown at different times, these treatments were not directly compared.

Plants were grown for five weeks at the selected soil and air temperatures, then harvested. Total plant dry weights were determined as before. Total plant growth rates were calculated by subtracting initial dry weight from final dry weight, then dividing by number of days grown at the temperature treatments.

Net photosynthesis and dark respiration rates were measured in a closed system with a LI-6200 portable infrared gas analyzer (IRGA) on several dates. Measurements were made in greenhouses between 9 and 11 a.m. One terminal leaflet from the first fully expanded leaf (5th from apex) was enclosed in a 1 liter Lexan chamber. Photosynthesis rate was calculated from the rate of CO_2 depletion in the chamber. Two consecutive

measurements were taken, then averaged to provide one observation for each leaf. Carbon dioxide concentration ranged from 300 to 350 ppm, and light levels were 900 to 1200 $\mu\text{E m}^{-2} \text{ s}^{-1}$.

Dark respiration rates were also measured on leaflets from the first fully-expanded leaf. The entire chamber and plant were enclosed in black plastic to exclude light. Leaflets were equilibrated for 5 min in the dark, then respiration rate was determined from the rate of increase in chamber CO_2 concentration over two consecutive 1 min intervals. The two measurements were averaged to provide one observation for each leaf. The entire system was shaded from direct light during measurements to prevent chamber heating. However, chamber temperatures fluctuated with greenhouse temperature, and were 21 to 26°C in the low temperature greenhouse and 31 to 39°C in the high temperature greenhouse. Net photosynthesis and dark respiration of leaflets from plants of one replication were measured on each of four successive days. Respiration/photosynthesis ratios were calculated by dividing each respiration measurement by the photosynthesis measurement for the same leaf, and multiplying by 100.

Gross photosynthesis rates were also measured with an isotope porometer (IP) on leaflets subtending the terminal leaflet of the 4th or 5th leaf from the apex. Measurements were conducted between 9 and 11 a.m.

^{14}C Partitioning

Potato tubers of Russet Burbank, Desiree, LT-1 and DTO-28 were sprouted and seedpieces were planted into flats containing a sand, vermiculite, and peat moss soil moisture (2:2:1 by volume). Plants were grown in a greenhouse at 25°C day/12°C night temperature and 12 h photoperiod. Natural light level was supplemented with a mixture of metal halide and fluorescent lights. Uniform seedlings were transplanted into 6.6 liter pots containing the same soil mixture. All plants were placed in growth chambers (25/12°C, 12 h photoperiod) after transplanting. Approximately two weeks after tuber

initiation, three groups of plants were selected based on uniformity of height and leaf number. Three plants (replications) of each clone were harvested the same day (harvest I) and separated into vines, tubers, and roots with stolons; dried at 105°C for 2 to 6 h, then at 70°C for 3 days prior to weighing.

Remaining plants were placed in growth chambers and exposed to day/night temperatures of 25/12°C (control) or 35/25°C (heat stress). Light level (PAR, 400-700 nm) at the upper leaves was 350-450 $\mu\text{E m}^{-2} \text{s}^{-1}$ and the photoperiod was 12 h. Light was provided with a mixture of incandescent and fluorescent lights. All agronomic practices recommended for potatoes were followed, including fertilizing based on petiole tissue analysis (31). Plants were watered to excess twice daily to avoid water stress.

After two weeks in growth chambers, 16 plants of each clone (eight of each growth temperature) were labeled with $^{14}\text{CO}_2$ by the method of Gawronska et al. (11,12). During labeling the most recently mature leaf (fourth or fifth from apex) was enclosed for 30 min in a plastic bag with $^{14}\text{CO}_2$ generated by addition of sulfuric acid to sodium carbonate. All exposures were done between 0800-1100 h at 25°C and light levels between 300-350 $\mu\text{E m}^{-2} \text{s}^{-1}$. After labeling, temperatures in the heat stress chamber were returned to 35/25°C. Plants were harvested either 20 h after labeling (harvest II) or 15 days after labeling (harvest III). Plants were separated into vines, tubers and roots with stolons. Labeled plants were harvested at exactly 20 h or 15 days after exposure (in same order as exposure schedule) to insure the same time for translocation of ^{14}C -assimilates in each plant. Plant material was oven dried at 105°C for 2 to 6 h, then at 70°C for 3 days and dry weights recorded. Plant material was ground into a fine powder and two 50 mg subsamples from each organ were oxidized. Radioactivity was measured with a scintillation spectrometer.

Results

Soil temperature did not significantly affect leaf respiration rates. Net photosynthesis rates were reduced by high soil temperatures on several dates. However, there was no soil temperature x clone interaction. Therefore, data are presented as means of two soil temperatures.

Photosynthesis and Respiration

DTO-28 and NDA1725-1 produced more total dry matter at the final harvest and had higher growth rates than other clones at both low and high greenhouse air temperatures (Table 1). Russet Burbank produced the lowest dry matter of all clones under high greenhouse temperatures.

Desiree and Katahdin generally had higher dark respiration rates than DTO-28, NDA1725-1 and Russet Burbank (Table 1). Mean dry weights and growth rates of the six clones were related to dark respiration rates. Clones that produced the highest dry weights and growth rates had lower respiration rates than clones with low dry matter production. The exception was Russet Burbank grown at high greenhouse temperatures. Russet Burbank had low dry matter production, and also low dark respiration rates when grown at high temperatures. Simple linear correlation coefficients between total dry weight or growth rates and dark respiration rates were always negative, and significant at the 0.05 or 0.01 levels for plants grown at low temperature ($r = -0.82$ to -0.99). Dry matter production and respiration rates of the six clones were not significantly correlated at high greenhouse temperature ($r = -0.10$ to -0.31).

In general, clones having high photosynthetic rates with the IP also showed higher rates with the IRGA as well. Katahdin had significantly higher net photosynthesis rates (measured with IRGA) than other clones at low greenhouse air temperature (Table 1). At the high greenhouse temperature, all clones except Russet Burbank had similar net photosynthesis rates.

Comparison among clones at low greenhouse air temperatures showed that DTO-28 and DNA1725-1 had significantly higher gross photosynthetic rates (measured with IP) initially, compared to Russet Burbank (Table 2). The photosynthetic rates in DTO-28 then declined significantly at week 2 and were less than NDA1725-1 and Katahdin thereafter. At high greenhouse temperatures Desiree and Kennebec had significantly higher gross photosynthetic rates at cool soil temperature at week 3 compared to all other clones and at week 4 compared to Russet Burbank (Table 3).

Clones having high net photosynthesis rates also tended to have high respiration rates. NDA1725-1 was one of the exceptions, having relatively high net photosynthesis and low respiration rates. Clones exhibited differences in respiration/photosynthesis ratios. DTO-28 and NDA1725-1 had lower ratios than other clones.

¹⁴C Partitioning

DTO-28 and LT-1 produced the highest total plant dry weights at both temperatures (Figure 1). High temperature reduced total dry matter production at harvest III less in DTO-28 than in other clones. DTO-28 and LT-1 produced higher vine dry weights at both temperatures than Russet Burbank or Desiree (Figure 1). High temperature increased vine dry matter production less in Desiree and Russet Burbank than in DTO 28 and LT-1. DTO-28 and LT-1 produced higher tuber dry weights at low growth temperature than Desiree or Russet Burbank. However, DTO-28 and LT-1 also had a larger decrease in tuber dry weight at high temperature than other clones.

Plants grown at high temperature contained 51 to 68% of total dry matter in vines at harvest III, while those grown at low temperature contained only 35 to 45%. Russet Burbank partitioned a lower percentage of total dry matter to vines at both growth temperatures than other clones (Table 4). Plants grown at high temperature contained 14 to 40% of total dry matter in tubers at harvest III, while those grown at low temperature contained 52 to 62%. Russet Burbank had a higher proportion of total dry matter in tubers at both growth temperatures than other clones.

Fifteen days after labeling there was a higher percentage of ^{14}C in labeled leaves of plants grown at high temperature (Table 4). All clones contained approximately the same percentage of ^{14}C in labeled leaves. Fifteen days after labeling tubers contained an average of 58% of the ^{14}C at low temperature, but only 24% at high temperature. Russet Burbank partitioned a higher percentage of the ^{14}C to tubers at high temperature than other clones.

Discussion

The photosynthetic rates recorded with the isotope porometer (IP) were generally higher than those recorded with the infra-red gas analyzer (IRGA) in all clones probably due to: (1) the IP measured gross photosynthesis while the IRGA measured net photosynthesis, and (2) the leaf chamber used with the IRGA reduced the incident radiation reaching the leaf.

High photosynthetic rates do not necessarily translate into higher dry matter accumulation. Generally, photosynthetic rates did not correspond with rates of dry matter accumulation. For example, Katahdin had high rates of photosynthesis but low dry matter accumulation. DTO-28 had low gross photosynthesis rates, but had comparatively higher dry matter accumulation compared to other clones. Since dry matter accumulation in plants is affected by several factors other than photosynthesis, it should be realized that dry matter may not always correlate with single leaf photosynthesis (9).

Dark respiration rates did not explain all differences in heat tolerance among clones. Russet Burbank, a heat sensitive clone, had respiration rates as low as several heat tolerant clones (DTO-28 and NDA1725-1). In contrast, Wivutvongvana (33) reported that heat tolerant clones of *Solanum acaule* and *chacoense* had lower respiration rates than sensitive clones. Heat tolerant genotypes of *Atriplex lentiformis*

(25) and *Lolium perenne* (32) also have lower leaf dark respiration than heat sensitive genotypes. Apparently low leaf dark respiration is not an exclusive characteristic of heat tolerant potato clones.

Potato clones with high net photosynthesis rates also tended to have high dark respiration rates. However, there were several exceptions to this relationship, and correlations were generally not significant. Volence et al. (30) reported similar results for tall fescue genotypes. They concluded that photosynthesis and respiration were genetically independent, indicating that breeding for low respiration or high photosynthesis rates would not be compounded by undesirable changes in other gas exchange characteristics. DTO-28 and NDA1725-1, both heat tolerant, had lower respiration/photosynthesis ratios than other clones on several dates. Reduced supply of assimilates for growth and maintenance of plant tissues is one of the primary effects of heat stress (14). Efficient use of fixed carbon would be an important characteristic of heat tolerant clones if tuber yield is source limited at high temperatures. However, not all differences in heat tolerance can be explained by respiration/photosynthesis ratios. Desiree has been classified as heat tolerant by several authors (15,22). Desiree generally had high respiration/photosynthesis ratios, and had relatively low growth rates at high temperature compared to other heat tolerant clones. Desiree may be heat tolerant under field conditions because it initiates tubers earlier at high temperatures than sensitive clones (15).

Plants grown at low temperature exported more ^{14}C -labeled assimilate out of leaves than those at high temperature. Dinar et al. (6,7) observed inhibited assimilate transport from leaves of both heat sensitive and tolerant tomato cultivars within 72 h after exposure to heat stress. Reduction in assimilate export from leaves at high temperature could be due to inhibition of transport, increased use of assimilate for growth and maintenance in source leaves, or reduced sink demand. Dinar et al. (6) attributed reduced transport in tomato plants exposed to heat stress to formation of callose in

phloem sieve tube plates of leaf petioles. Benoit et al. (3) claim that at high temperature a greater proportion of daily carbon uptake would be utilized for maintenance of foliage, leaving little assimilate for growth of sinks. Krauss and Marschner (13) found that heating individual tubers to 30°C stopped tuber growth, without affecting the supply of assimilates.

Growth temperature also affected distribution of ^{14}C assimilates. At low temperature ^{14}C assimilates were transported mainly to tubers. Over 70% of ^{14}C assimilates exported out of labeled leaves was recovered from tubers 15 days after labeling. This value is comparable to those observed by Gawronska and Dwelle (12) for Russet Burbank grown in a greenhouse, and by Gawronska et al. (11) for field grown Russet Burbank.

Under high temperature the proportion of ^{14}C assimilate partitioned to tubers decreased with time after labeling, and was smaller than under low temperature. A larger proportion of ^{14}C assimilates partitioned to tubers at high temperature were probably released through respiration.

Although there were consistent differences among clones in export of ^{14}C assimilates from labeled leaves at both growth temperatures, these differences were not related to total dry matter accumulation. Clones exported a similar portion of ^{14}C assimilates out of labeled leaves when grown at low temperature. However DTO-28 and LT-1 accumulated more dry matter over the four week treatment. At high temperature Desiree and Russet Burbank exported more ^{14}C assimilate from the labeled leaves than DTO-28 and LT-1, even though the latter clones had higher overall growth rates. Export of ^{14}C assimilate from labeled leaves is strongly affected by plant growth stage (11,12). Thus, these differences in export rates could represent differences in stage of plant development, rather than differences in demand for assimilate.

DTO-28 and LT-1 partitioned more ^{14}C assimilate to tubers at low temperature than other clones, and also produced the highest tuber yields. Russet Burbank

partitioned more dry matter and ^{14}C assimilates to tubers at high temperature than other clones. Dinar and Rudich (7) reported that transport of assimilate from leaves to roots in tomato was affected more by temperature in heat sensitive than heat tolerant cultivars. Russet Burbank is not generally considered a heat tolerant cultivar (2), and its ability to export carbon out of leaves to tubers at high temperature may have been related to its development of a relatively large tuber biomass before stress began (36% vs 6 to 15% for other clones).

In summary, several heat tolerant clones had low respiration rates, and relatively high net photosynthesis rates at both growth temperatures. Consequently these clones had low respiration/photosynthesis ratios, indicating more efficient use of fixed carbon. Combining measurements of several physiological traits (photosynthesis, respiration and ^{14}C partitioning) did not explain all genotypic variation in stress tolerance. This is not surprising because heat stress reduces tuber yields by affecting several plant processes in addition to carbon assimilation and partitioning (7,13). Tuber initiation is also a limiting factor at high temperatures. However, determination of respiration/photosynthesis ratios may help explain the physiological basis for heat tolerance of some clones.

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Table 1. Relationship between leaf dark respiration (Rd), photosynthesis (Ps), and growth rates of six potato clones grown at two temperature regimes. Photosynthesis and respiration rates were measured with an infrared gas analyzer.

Clone	Greenhouse Temp (°C)	Total Growth Rate (g plant ⁻¹ d ⁻¹)	Rd (umole CO ₂ m ⁻² s ⁻¹)	Ps (umole CO ₂ m ⁻² s ⁻¹)	Rd/Ps ^y (%)
Katahdin	25/12°C	2.7 d ^z	3.1 ab	17.0 a	17.5 ab
Desiree		3.2 c	3.1 ab	11.2 b	25.3 a
Kennebec		3.4 c	3.4 a	12.2 b	24.3 ab
Russet Burbank		3.6 bc	2.7 abc	11.8 b	22.8 ab
DTO-28		4.1 ab	2.1 c	11.3 b	17.0 ab
NDA1725-1		4.4 a	2.5 bc	14.2 ab	16.5 b
Russet Burbank	38/28°C	2.0 c	1.7 c	14.3 b	16.3 ab
Desiree		2.3 bc	2.8 b	15.3 ab	18.5 ab
Katahdin		2.4 b	2.5 b	21.6 a	12.3 b
Kennebec		2.4 b	3.2 a	18.4 ab	20.0 a
DTO-28		2.7 a	2.1 c	19.8 ab	11.1 b
NDA1725-1		2.8 a	2.0 c	17.9 ab	12.1 b

y Respiration/photosynthesis ratio, (Rd/Ps)*100.

z Means within columns followed by different letters are significantly different (p=0.05) by DMRT.

Table 2. Gross photosynthetic rates (P_G) of six potato clones grown at low greenhouse temperatures. Measurements were taken with the isotope porometer at air temperatures of 22 to 29°C.^{1/}

Clone	Gross Photosynthetic Rates (mg CO ₂ dm ⁻² hr ⁻¹)				
	Time Interval				
	Initial	Week 1	Week 2	Week 3	Week 4
	Soil Temperature (C)				
Russet Burbank	39	34	43	48	48
Desiree	44	36	55	50	51
Kennebec	42	37	51	54	56
DTO-28	47	42	32	35	41
NDA1725-1	49	35	54	56	57
Katahdin	44	35	56	57	60
^{2/} LSD 5%	7	7	10	11	10

^{1/} Values are means of 8 readings.

^{2/} LSD for clones (mean values)

Table 3. Gross photosynthetic rates (P_G) of six potato clones grown at high greenhouse temperatures. Measurements were taken with the isotope porometer at air temperatures of 31 to 39°C.^{1/}

Clone	Gross Photosynthetic Rates (mg CO ₂ dm ⁻² hr ⁻¹)				
	Initial	<u>Week 1</u>	Time Interval		<u>Week 4</u>
			<u>Week 2</u>	<u>Week 3</u>	
			Soil Temperature (C)		
Russet Burbank	40	46	37	20	14
Desiree	56	49	41	35	28
Kennebec	56	54	42	35	25
DTO-28	42	49	38	33	20
NDA1725-1	58	55	42	29	24
Katahdin	64	57	49	27	21
2/LSD 5%	13	13	9	9	5

^{1/} Values are means of 8 readings.

^{2/} LSD for clones (mean values)

Table 4. Dry matter and ^{14}C assimilate distribution patterns 15 days (harvest III) after labeling in separate organs of four potato clones grown at two temperature regimes.

Clone	Growth Chamber Temperature (°C)	Dry Weight (% of Total)		^{14}C (% of Total)	
		Vines	Tubers	Labeled Leaf	Tubers
Russet Burbank	25/12	35.2	62.0	19.9	55.6
Desiree		44.4	51.8	18.5	50.0
LT-1		39.9	56.7	20.6	57.4
DTO-28		45.6	51.5	16.6	67.4
Russet Burbank	35/25	51.3	39.3	21.2	41.5
Desiree		68.0	16.3	22.8	21.6
LT-1		61.5	21.9	32.1	19.2
DTO-28		60.5	24.1	27.8	15.6

Figure 1. Dry matter accumulation in separate organs of 4 potato clones grown at (A) 25/12°C or (B) 35/25°C. Harvest I -- start of temperature treatments, Harvest II -- 2 weeks after start, Harvest III -- 4 weeks after start.

1997-1998
1998-1999
1999-2000

(25/12°C)

26

(35/25°C)

Variation in patterns of osmotic regulation and proline concentration and their association with dry matter production and partitioning in potatoes (*Solanum tuberosum* L.) exposed to transient heat and drought stress.

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Abstract

Potato plants (Solanum tuberosum L.) of cvs. Alpha, Cara, Desiree, Blanka, and Idit were exposed to a transient heat or drought stress during the period of tuber growth. Confounding effects of heat stress with drought stress were minimized in an attempt to study the specific response to each of these stresses. Both heat and drought reduced dry matter production and the partitioning of dry matter to the tubers.

Heat stress did not affect the osmotic potential, the content of total soluble solids (TSS), or the content of proline in the leaves or tubers of any of the five cultivars. Drought stress reduced the osmotic potential in both leaf and tuber tissue, and this was accompanied by an increase in the content of TSS. A temporary contribution of TSS to the osmotic potential of young expanding leaves was induced by drought being the most distinct in the cv Idit. This might be associated with the lower losses of tuber dry matter due to transient drought, and indicate adaptation to drought.

Water deficit increased proline content in both leaf and tuber tissue. Upon stress relief, the content of proline in the leaf tissue of the stressed plants was reduced to levels comparable to those in the leaves of the control plants, but the content in the tuber tissue of the stressed plants was maintained at a higher level. The pattern of the change of the proline content in the tuber tissue of stressed plants differed among the cultivars; in

Idit and Alpha, there was a steady decline upon stress relief while in the three other cultivars its content fluctuated. In these two cultivars, the dry matter concentration in tubers was also higher than in the three other cultivars. This phenomenon might be related to an improved capacity to recover from stress indicated by the pattern of proline metabolism upon stress relief.

Introduction

Cultivated potatoes (Solanum tuberosum L.) are very susceptible to heat (1, 3, 4) and to drought (6, 21). In many arid and semi-arid regions, potatoes are exposed to high temperatures combined with a comparatively dry atmosphere. High temperature stress is a major uncontrolled factor affecting growth, development and productivity of plants, and the adverse effect of high temperature on potato tuber yield and quality is a major obstacle for potato production in hot regions. Drought, is another common stress to which potatoes are exposed in regions where water sources are limited. Thus, the study of genetic variation in the response and adaptation to stress is important.

Several mechanisms were mentioned as involving the adaptation of plants to stress (9, 19, 20). Turgor maintenance under stress conditions was suggested to enable the continuation of growth, and osmotic adjustment is considered one of the mechanisms assisting in the maintenance of turgor. Sugars and amino acids

are major constituents of osmoregulation (11, 19). In green leaves, expanded but still growing, an increase in sugars and amino acids presumably is affected by the difference between the rate of carbon fixation and the rate of its export (11). However, in a non-photosynthetic expanding organ, e.g. the potato tuber, osmoregulation is dependent on the import of solutes, except for proline, which accumulates in detached tubers (18). The significance of high proline levels to the stressed plant is still a matter of dispute and it is difficult to prove whether this compound has an important adaptive role. According to Hanson and Hitz (5) unless genetic variation can be found for a metabolic response to stress, it cannot be used in selection and breeding of tolerant cultivars.

Although much attention has been given to studying the adverse effects of stress, there is not much information on the physiological and metabolic responses of potatoes to stress. In the present study we examined changes occurring during a) transient heat stress (HS) or drought stress (WS) and b) after stress relief during recovery. Patterns of dry matter (DM) accumulation and partitioning as well as the concomitant changes in the content of total soluble solids (TSS) and proline, which presumably play a role in adaptation to stress, were monitored. Also, five different genotypes were included in the experiment in an attempt to explore possible varietal differences in the relationships between these metabolic changes and stress susceptibility or tolerance.

Materials and methods

Single main stems of the potato (*Solanum tuberosum* L.) cvs Alpha, Cara, Desiree, Blanka and Idit were placed in 10-l pots containing tuff and peat (4:1 v/v) and grown in the open. A single layer of white coarse net was hung ca 2 m above the soil and covered the plants from above and on the sides in order to reduce aphid incidence. The plants were irrigated with ample amounts of nutrient solution containing N:P:K (20:20:20) every 1-2 days for 44 days. Prior to the stress treatments, the plants of each of the five cultivars were divided into three groups of 20 plants each. One group served as control and was irrigated with water regularly. In the second group of each of the cultivars, water deficit was induced by withholding irrigation for 6 days, by which time over 50% of the leaves had wilted. Thereafter, stress was relieved by watering, and 26 days later haulm and tubers were harvested. The third group of each of the cultivars was placed for 12 days in a glasshouse and exposed to a daytime temperature of 37-39°C (13 h) and a night temperature of 23-25°C. The plants were irrigated twice a day to avoid WS during the exposure to HS; this was confirmed by the similar or less negative water potentials measured in the leaves of the plants exposed to the HS as compared with those recorded in the control plants. After the heat treatment, the plants were replaced under the white coarse net, grown under ambient conditions for 18 days, and then harvested. The mean maximum day temperatures and the mean minimum night temperatures during the experiment period

were, respectively, 21.3° and 6.8°C in March, 24.0° and 10.1°C in April, 27.5° and 15.0°C in May, and 29.3° and 17.3°C in June. Water was withheld from the plants exposed to the WS from May 3-8, and plants were exposed to the HS in the glasshouse from May 3-15.

Measurements were conducted on expanding leaves, no. 4, 5 or 6 from the top. Five leaves of each cultivar were measured in each treatment. In the WS plants, non-wilting leaves were sampled, except on the 6th day of the drying period, when these leaves had started to wilt.

Water potentials were measured in a pressure chamber (PMS Instrument Co., Corvallis, OR, U.S.A) (13). Osmotic potentials were measured with an osmometer (model 2007, Precision Systems, Inc., Sudbury, MA, U.S.A) operated using the freezing point depression. TSS was estimated with a refractometer (Optimat, Japan) with a precision of 0.2% sucrose (14).

Proline was determined according to Singh et al (16). Samples of at least 250 mg fresh weight were taken from five leaves or from the outer storage parenchima of 15 tubers for each of these measurements. Dry weights of haulm and tubers were determined by placing the haulm of each plant in a paper bag and at least 200g of tuber tissue in a glass beaker in a ventilated oven set to 75°C for at least 48 h. Three or four plants of each treatment were sampled except at the last sampling (harvest), at which time the haulm of six plants and the tubers of ten plants in each

Results

Withholding water for 6 days, until signs of leaf-wilting were evident, tended to increase the DM weight of the haulm (Figs. 1, 2). After the resumption of irrigation, a retardation of dry matter (DM) accumulation in the haulm was observed, being the most distinct in cv. Desiree (Fig. 2). On the other hand, in cv. Cara, a single cycle of transient WS had practically no inhibitory effect on haulm growth (Fig. 1). The accumulation of DM in tubers was retarded by WS, resulting in a lower DM yield in tubers throughout the entire growing period (Figs 1, 2).

Heat stress inhibited the accumulation of DM in both haulm and tubers (Figs. 3, 4). A resumption of haulm growth was observed upon relief from HS. However, the accumulation of DM in the tubers was inhibited throughout the growing period (Figs. 3, 4). The control plants of Alpha and Cara, which are late-maturing cultivars, accumulated larger amounts of DM in the haulm as compared with Desiree (an intermediate-maturing cultivar) and to Blanka and Idit (early maturing) (Figs. 3, 4; Table 1).

Partitioning of DM was altered by stress. Growth retardation of the haulm imposed by heat stress, was followed by enhanced growth upon stress relief (Figs. 3, 4) and resulted in the enhancement of DM accumulation in the haulm (Table 1, dry weight and DM partitioning of HS). On the other hand, tuber growth was inhibited both during the heat stress period and after stress relief (Figs. 3, 4). It seems that the sink forces of the haulm

of plants exposed to the heat were stronger than the tuber sink. These differential sink forces not only retarded tuber growth (fresh weight), but also reduced the relative DM content in the tubers (Table 1). This was especially evident with plants exposed to HS.

Few data are available on the physiological and metabolic responses of potatoes to heat and drought stress, and data on the effect of high temperature stress under non limiting water supply are scarce. In the present study, measurements of leaf water potential indicated that no drought stress whatsoever occurred during the HS treatments (Table 2). In consequence, HS did not affect the osmotic potential of leaf or tuber tissue (not shown).

As expected, WS lowered the leaf water potential (Table 2), and recovery was evident one day after the renewal of irrigation. Concomitantly, WS lowered the osmotic potential of both leaf and tuber tissue (last day of withholding water, WS (0), Tables 3, 4), and a recovery to control levels was observed after irrigation renewal. Changes in the TSS component which apparently affects the osmotic potential, agreed well with changes occurring in the osmotic potential of leaf (Table 3) and tuber tissue (Table 4).

Heat stress did not alter the concentration of proline in leaf or tuber tissue, but WS caused a significant increase in the proline

level in leaves and tubers of all five cultivars (Figs. 5, 6). Two days after the renewal of irrigation, proline levels in the leaves were similar to those of the control plants. On the other hand, higher proline level, as compared with the control plants, was maintained in the tubers of all cultivars after stress relief. In Idit, Blanka and Desiree, the relatively early maturing cultivars, higher proline levels were still evident in the tubers 26 days after stress relief. In Cara and Alpha, the later maturing cultivars, the proline levels 26 days after stress relief were closer to those in tubers of the control plants (Fig. 6).

Discussion

Environmental stresses, such as drought and high temperatures, are major factors affecting plant growth and development and, consequently, crop yields. Traditionally, potatoes have been classified as a cool season crop, 17°-20°C being widely accepted as optimal mean temperatures for net photosynthesis (3). Over the last two decades, the potato has rapidly migrated to tropical and subtropical areas of the world, becoming one of the most valuable staple foods, due to its high nutritional value (7). However, potato cultivars bred in the temperate climates of Europe and North America, when exposed to the environmental constraints, namely, high temperatures and water shortage prevailing in arid and semi-arid regions, are adversely affected. Thus, studies of varietal differences in adaptation to stress, as well as mechanisms involved in it are of importance.

It is worth noting that under field conditions in these regions, effects of HS are often confounded with those of WS, because drought is commonly accompanied by high temperatures and low air humidity (9). In the present experiments, confounding effects of HS with those of WS were minimized by the ample water supply and the high air humidity during the HS period. The values of leaf water potential measured in the plants during the HS (Table 2) indicate that the plants were not exposed to drought; thus, it is reasonable to assume that they reflect effects caused mainly by high temperatures.

The results of this study show the prominent role of high temperature stress in reducing DM accumulation and in altering partitioning leading to a significant reduction in tuber yields (Figs. 3, 4; Table 1). However, it is clearly shown that HS had no effect whatsoever on the osmotic potential (OP), on the content of TSS (Tables 3, 4) or on proline content (Figs 5, 6) provided drought was avoided. Hence, the adverse effects of high temperature are presumably associated with other physiological and metabolic events such as reduced photosynthesis, increased respiration, and shifting of hormonal and metabolic balance (3).

Water deficit induces lowering of the osmotic potential in some species and cultivars, thereby contributing to turgor maintenance as water potential decreases (19). Increases in the concentration of potassium, sugars and amino acids accounted for 60-100% of the osmotic adjustment observed in expanding leaves of wheat (12).

Lowering of the OP in response to drought was reported for potatoes, too, accompanied by an increase in the content of TSS in the tissue sap (10). Similar behaviour, i.e., an increase in TSS content concomitant with the lowering of OP, was observed in the present experiment in both leaf and tuber tissues (Tables 3, 4). Soon after stress relief, the OP and the TSS content of leaves and tubers of WS plants came close to those of the control plants (Tables 3, 4). However, in the expanding leaves of Idit, TSS content and its contribution to the OP was still indicated 14 days after stress relief (control 14 and WS14, Table 3). This adjustment occurred after the decrease in TSS content upon tissue rehydration, observed 2 days after stress relief (WS2, Table 3). This event seems to be associated with the relatively small loss in tuber dry weight in this cultivar (Table 1). It is worth noting that the differences in TSS content and in OP occurred between leaves and tubers in all the cultivars, being higher in the leaf tissue which was exposed to water loss through transpiration.

The accumulation of free proline in tissue of plants grown under stress is evident in many studies (2, 15, 17). In a previous study (10) it was suggested that proline accumulation in potato leaves is triggered by severe drought stress and no adjustment of proline content was observed during early stages of stress development. However, the possibility that proline could contribute to osmoregulation (22) cannot be dismissed. Jones et al. (8) suggested that proline could contribute to osmotic

adjustment if it was confined to the cytoplasm or some part thereof, although direct evidence that proline is so compartmented is lacking.

It is interesting to note that, although both leaves (Fig. 5) and tubers (Fig. 6) accumulated proline in response to water deficit, there was a difference in the pattern of its metabolism upon stress relief. Proline was rapidly metabolized and declined to the level of the control plants in the tissue of the expanding leaves when transferred from the dehydrated to the hydrated state (Fig. 5), while its content in the tuber tissue remained elevated after stress relief (Fig. 6). The biochemical mechanisms, induced by the transient drought stress and which caused this differential metabolic response of leaf vs tuber tissue, which are parts of the same plant, were not resolved. Furthermore, if proline does play a role in the adaptive response of potatoes to drought, and if it is related to the relative tolerance of a certain variety to transient water deficit, as measured by the relative loss of DM yield, it is probably mantled by the complexity of the biochemical mechanisms involved in dry matter production.

Although there are differences in the absolute levels of proline accumulated in the tuber tissue of the various cultivars, no obvious relationship is apparent with the relative loss of dry weight in tubers or in the whole plant (Table 1, Figs. 5, 6). However, it is worth noting that in Idit and Alpha tubers, there

was a steady decline in proline levels after stress relief vs a further increase or fluctuating content in the three other cultivars (Fig. 6). Concomitantly, the concentration of DM in the tubers of these two cultivars was higher than in the others (Table 1), probably reflecting inherent greater sink forces in Idit and Alpha tubers. This pattern of proline metabolism in tubers of Alpha and Idit might represent a capacity to respond promptly to stress as well as to relief, and this fast "responsiveness", might be related to the capacity to accumulate DM. Additional experiments with wider genotypic variation are desired to establish the possible association of "responsiveness" with tolerance to transient drought.

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Table 1. Dry matter yield and partitioning as affected by a single cycle of heat stress (HS) or drought stress (WS). Data collected at harvest, 18 and 26 days after the relief from WS and HS, respectively. Data for the haulm for the tubers are means of five and ten plants, respectively.

Cultivar	Plant part	Dry weight ₁ (DW) g plant ⁻¹ + SE		Dry matter partitioning % of total DM			Dry matter content % of fresh weight			DW loss % of contro	
		Control	HS	Control	HS	WS	Control	HS	WS	HS	WS
Alpha	Haulm	53+4	65+2	35	58	46	10.3	9.5	10.7	-	-
	Tubers	94+5	30+2	64	32	54	22.6	16.3	18.2	68	44
	Total	147	95	-	-	-	-	-	-	35	33
Cara	Haulm	53+2	55+3	42	67	57	10.0	9.3	9.9	-	-
	Tubers	72+4	27+3	58	33	43	15.2	10.9	12.7	52	40
	Total	125	82	-	-	-	-	-	-	34	21
Desiree	Haulm	31+2	60+5	25	65	47	11.0	11.1	10.8	-	-
	Tubers	94+4	33+4	75	35	53	18.4	13.4	15.4	65	48
	Total	125	93	-	-	-	-	-	-	26	25
Blanka	Haulm	25+2	39+7	22	56	32	11.4	9.5	12.5	-	-
	Tubers	88+9	31+4	78	44	63	18.2	12.1	14.3	55	34
	Total	113	70	-	-	-	-	-	-	38	25
Idit	Haulm	39+3	46+3	35	54	42	13.9	10.7	14.4	-	-
	Tubers	74+6	39+4	65	45	58	21.3	18.2	18.8	47	28
	Total	113	85	-	-	-	-	-	-	25	19

Table 2. The effect on leaf water potential of drought stress (WS) at the end of the WS treatment (6th day after withholding irrigation) and one day after the renewal of irrigation (day 7); and of high temperature stress (HS) 5 days after the commencement of the HS under conditions of ample water supply (Mpa + S.E.).

Cultivar	Control	WS		HS
		day 6	day 7	day 5
Alpha	-0.9 7±0.3	-1.5 5±0.3	-0.9 3±0.2	-0.7 1±0.3
Cara	-0.7 2±0.2	-1.5 1±0.3	-0.8 1±0.3	-0.6 0±0.4
Desiree	-0.6 4±0.3	-1.4 6±0.3	-0.9 2±0.3	-0.6 7±0.3
Blanka	-0.9 0±0.5	-1.4 9±0.2	-0.9 8±0.5	-0.5 9±0.2
Idit	-0.7 3±0.4	-1.9 1±0.4	-0.9 0±0.3	-0.5 7±0.2

Table 3. The contribution of total soluble solids (TSS) to the osmotic potential (OP) of potato leaves in plants subjected to a single cycle of drought (WS). Numbers in parenthesis are days after stress relief.

Cultivar	Trait	Control (0)	WS (0)	WS (2)	Control (14)	WS (14)	Control (26)	WS (26)
Alpha	Osmotic potential (-MPa)	1.65 $\pm$ 0.03	1.83 $\pm$ 0.03	1.40 $\pm$ 0.05	1.42 $\pm$ 0.09	1.29 $\pm$ 0.06	1.34 $\pm$ 0.01	1.43 $\pm$ 0.09
	TSS content (%)	4.8 $\pm$ 0.2	6.7 $\pm$ 0.2	4.9 $\pm$ 0.1	4.8 $\pm$ 0.3	4.1 $\pm$ 0.3	5.0 $\pm$ 0	5.4 $\pm$ 0.2
	MPa due to TSS	0.37	0.51	0.375	0.36	0.30	0.38	0.44
	Contribution of TSS to OP (%)	22.4	27.9	26.8	25.4	23.3	28.3	30.1
Cara	Osmotic potential (-MPa)	1.55 $\pm$ 0.07	1.90 $\pm$ 0.13	1.46 $\pm$ 0.02	1.11 $\pm$ 0.03	1.17 $\pm$ 0.02	1.23 $\pm$ 0.04	1.23 $\pm$ 0.03
	TSS content (%)	4.2 $\pm$ 0.1	6.0 $\pm$ 0	4.8 $\pm$ 0.2	3.2 $\pm$ 0.6	3.3 $\pm$ 0.2	3.4 $\pm$ 0.2	3.4 $\pm$ 0.2
	MPa due to TSS	0.32	0.47	0.37	0.25	0.25	0.26	0.26
	Contribution of TSS to OP (%)	20.6	24.7	25.3	22.5	21.4	21.1	21.1
Destree	Osmotic potential (-MPa)	1.38 $\pm$ 0.02	1.77 $\pm$ 0.10	1.51 $\pm$ 0.01	1.37 $\pm$ 0.02	1.32 $\pm$ 0.02	1.40 $\pm$ 0.02	1.34 $\pm$ 0.03
	TSS content (%)	4.31 $\pm$ 0	6.2 $\pm$ 0.2	5.3 $\pm$ 0.2	3.7 $\pm$ 0.1	4.2 $\pm$ 0.2	4.7 $\pm$ 0.1	3.9 $\pm$ 0.6
	MPa due to TSS	0.33	0.475	0.406	0.29	0.32	0.36	0.30
	Contribution of TSS to OP (%)	23.9	26.8	26.9	21.2	24.2	25.7	22.4
Blanka	Osmotic potential (-MPa)	1.50 $\pm$ 0.16	1.76 $\pm$ 0.04	1.43 $\pm$ 0.07	1.45 $\pm$ 0.08	1.38 $\pm$ 0.06	1.48 $\pm$ 0.02	1.33 $\pm$ 0.04
	TSS content (%)	4.2 $\pm$ 0.3	6.1 $\pm$ 0.1	4.5 $\pm$ 0.2	4.5 $\pm$ 0.5	4.8 $\pm$ 0.1	5.3 $\pm$ 0.2	4.2 $\pm$ 0.2
	MPa due to TSS	0.32	0.466	0.34	0.34	0.37	0.406	0.32
	Contribution of TSS to OP (%)	21.3	26.5	23.8	23.4	26.8	27.4	24.1
Idit	Osmotic potential (-MPa)	1.83 $\pm$ 0.02	1.90 $\pm$ 0.03	1.72 $\pm$ 0.07	1.38 $\pm$ 0.03	1.81 $\pm$ 0.04	1.68 $\pm$ 0.06	1.56 $\pm$ 0.03
	TSS content (%)	6.1 $\pm$ 0.2	7.2 $\pm$ 0.2	5.0 $\pm$ 0	4.5 $\pm$ 0.3	6.5 $\pm$ 0.2	5.8 $\pm$ 0.1	5.0 $\pm$ 0.2
	MPa due to TSS	0.466	0.55	0.38	0.34	0.50	0.44	0.38
	Contribution of TSS to OP (%)	25.5	28.9	22.1	24.6	27.6	26.2	24.4

Table 4. The contribution of total soluble solids (TSS) to the osmotic potential (OP) of potato tubers in plants subjected to a single cycle of drought (WS). Numbers in parenthesis are days after stress relief.

Cultivar	Trait	Control(0)	WS (0)	WS (1)	WS (13)	Control (25)	WS (25)	Control (34)	WS (34)
Alpha	Osmotic potential (-MPa)	1.04 $\pm$ 0.01	1.61 $\pm$ 0.04	0.95 $\pm$ 0.02	1.09 $\pm$ 0.04	1.04 $\pm$ 0.03	1.09 $\pm$ 0.04	0.34 $\pm$ 0	0.34 $\pm$ 0
	TSS content (%)	3.9 $\pm$ 0.1	6.3 $\pm$ 0.3	3.4 $\pm$ 0	3.7 $\pm$ 0	3.5 $\pm$ 0.2	3.7 $\pm$ 0	3.0 $\pm$ 0	3.0 $\pm$ 0
	MPa due to TSS	0.29	0.48	0.25	0.28	0.27	0.28	0.23	0.23
	Contribution of TSS to OP (%)	27.9	29.3	27.4	25.7	26.0	25.7	27.3	27.3
Cara	Osmotic potential (-MPa)	0.99 $\pm$ 0.08	1.30 $\pm$ 0.03	0.92 $\pm$ 0.03	0.84 $\pm$ 0.02	0.82 $\pm$ 0.02	0.92 $\pm$ 0.01	0.75 $\pm$ 0.01	0.32 $\pm$ 0.03
	TSS content (%)	3.6 $\pm$ 0.1	5.3 $\pm$ 0.2	3.5 $\pm$ 0	2.9 $\pm$ 0	2.9 $\pm$ 0	3.2 $\pm$ 0.1	2.5 $\pm$ 0	2.7 $\pm$ 0
	MPa due to TSS	0.27	0.405	0.27	0.22	0.22	0.24	0.17	0.206
	Contribution of TSS to OP (%)	27.3	31.2	29.3	26.2	26.8	26.1	22.7	25.1
Desiree	Osmotic potential (-MPa)	1.04 $\pm$ 0.03	1.34 $\pm$ 0.04	0.94 $\pm$ 0.02	1.01 $\pm$ 0.02	0.94 $\pm$ 0.05	0.99 $\pm$ 0.02	0.37 $\pm$ 0.01	1.04 $\pm$ 0.15
	TSS content (%)	3.6 $\pm$ 0	5.7 $\pm$ 0.3	4.0 $\pm$ 0	4.0 $\pm$ 0	3.5 $\pm$ 0.1	3.3 $\pm$ 0	3.2 $\pm$ 0	3.5 $\pm$ 0.3
	MPa due to TSS	0.27	0.435	0.305	0.305	0.27	0.27	0.24	0.27
	Contribution of TSS to OP (%)	26.0	32.5	32.5	30.3	28.7	27.3	27.5	25.0
Blanka	Osmotic potential (-MPa)	0.98 $\pm$ 0.05	1.24 $\pm$ 0.04	0.95 $\pm$ 0.01	0.92 $\pm$ 0.04	0.93 $\pm$ 0.01	0.98 $\pm$ 0.02	0.37 $\pm$ 0.1	0.81 $\pm$ 0.04
	TSS content (%)	3.9 $\pm$ 0	4.7 $\pm$ 0.1	3.5 $\pm$ 0	3.5 $\pm$ 0	3.1 $\pm$ 0	3.6 $\pm$ 0	3.3 $\pm$ 0.1	3.2 $\pm$ 0
	MPa due to TSS	0.29	0.36	0.27	0.27	0.24	0.27	0.25	0.24
	Contribution of TSS to OP (%)	29.6	29.0	23.4	29.3	27.0	27.6	23.7	29.5
Idit	Osmotic potential (-MPa)	1.01 $\pm$ 0.04	1.37 $\pm$ 0.04	1.15 $\pm$ 0.01	1.05 $\pm$ 0.01	1.15 $\pm$ 0.03	1.30 $\pm$ 0.13	1.07 $\pm$ 0.07	1.04 $\pm$ 0.05
	TSS content (%)	3.9 $\pm$ 0.1	5.2 $\pm$ 0.1	4.7 $\pm$ 0.1	4.0 $\pm$ 0	4.6 $\pm$ 0.1	4.9 $\pm$ 0.2	4.2 $\pm$ 0.3	4.0 $\pm$ 0
	MPa due to TSS	0.29	0.475	0.35	0.305	0.35	0.375	0.32	0.305
	Contribution of TSS to OP (%)	28.7	34.7	31.3	29.1	30.2	28.3	29.9	29.4

Figure Legends

Figure 1: The effect of a transient drought stress (WS, dark symbols) on dry matter accumulation in haulm (circles) and tubers (triangles) of potatoes cvs. Cara and Alpha. Clear symbols represent the control plants.

Vertical bars represent standard error.

Figure 2: The effect of a transient drought stress (WS, dark symbols) on dry matter accumulation in haulm (circles) and tubers (triangles) of potatoes cvs. Desiree, Blanka and Idit. Clear symbols represent the control plants. Vertical bars represent standard error.

Figure 3: The effect of transient heat stress (HS, dark symbols) on dry matter accumulation in haulm (circles) and tubers (triangles) of potatoes cvs. Cara and Alpha. Clear symbols represent the control plants. Vertical bars represent standard error.

Figure 4: The effect of a transient heat stress (HS, dark symbols) on dry matter accumulation in haulm (circles) and tubers (triangles) of potatoes cvs. Desiree, Blanka and Idit. Clear symbols represent the control plants.

Vertical bars represent standard error.

Figure 5: The effect of a transient drought stress (WS) or heat stress (HS) on the content of proline in potato leaves. Vertical bars represent standard error.

Figure 6: The effect of a transient drought stress (WS) or heat stress (HS) on the content of proline in potato tubers. Vertical bars represent standard error.

Figure 3.

Figure 4.

Figure 6.

Evaluation of parents and selection for heat tolerance in the early generations of a potato (Solanum tuberosum L.) breeding program

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Summary

Potato cultivars (Solanum tuberosum L.) were evaluated for their capacity to form tubers under high temperature conditions (heat tolerance). In an experiment conducted in the hot summer season in the field, and in experiments conducted under controlled environments in glasshouses, differences in tolerance to heat were noted among the various genotypes. — Although heat tolerance tended to be associated with earliness in maturation, differences in the response to high temperatures were observed in genotypes of the same maturity class.

Progeny of the cultivars Desiree and Cara, and hybrid progeny of Cara X Desiree and of Blanka X Cara, were screened for heat tolerance in controlled environments in glasshouses. Long photoperiod delayed tuberization but high temperatures strongly inhibited tuber formation which was 4% in the progeny of Desiree, <2% in the progeny of Cara and of Cara X Desiree, and ca 16% in progeny of Blanka X Cara. For seedlings that did not form tubers in the hot glasshouse but were subsequently transferred to the cool glasshouse, tuberization was much enhanced, and clones selected through this dual procedure exhibited tolerance to heat in the first clonal year.

The results of this study indicate that: (a) tolerance to heat was associated with earliness; however, differences in the response to heat existed among late maturing cultivars; (b) tolerance to heat, as assessed by the capacity to form tubers under high temperatures, is genetically

controlled, and the timing of tuberization might be independent of the rate of tuberization in hybrid progeny; (c) the incidence of heat tolerance in progeny population is correlated with the relative tolerance of the parents; and (d) the dual selection procedure is an efficient approach for the selection of heat-tolerant clones.

Key Words : Cultivars -Families- Maturity classes - Selection efficiency -
Controlled Environment.

Introduction

Numerous potato cultivars, mostly S. tuberosum L. ssp. tuberosum, have been bred over the centuries in the temperate climates of Europe and North America, where centers for potato breeding and research flourished. The potato was considered to be adapted to cool climates and to be adversely affected by high temperatures (Borah and Milthorpe 1962, Hawkes 1978). Because of the more recent cultivation of potatoes in subtropical, semi-arid and arid regions, the need arose for breeding heat-tolerant cultivars (Simmonds 1971, Swaminathan and Sawyer 1983). Interestingly, although the modern ssp. tuberosum is extensively adapted to the conditions prevailing in temperate climates, namely, moderate day temperatures, cool nights and long days, certain genotypes have the capacity to initiate tubers at high temperatures (Ewing et al. 1987) and exhibit relatively small yield losses in hot seasons (Levy 1986a,b.). Recently, heat-tolerant accessions of S. bulbocastanum, S. chacoense, S. demissum and S. stoloniferum that could be used in breeding programs were identified (Reynolds and Ewing 1989). However, although high temperature stress is a major uncontrolled factor affecting growth, development and productivity of plants (Marshall 1982), relatively little is known about the genetic diversity for heat tolerance. Furthermore, tolerance to heat stress seems to involve many complex relationships, and an adapted genotype is expected to have a combination of genes for tolerance to high temperatures and for superior performance in the field. To achieve this goal, the breeder must evaluate an enormous number of genotypes and elaborate a reliable screening procedure for the efficient selection of heat tolerant clones in segregating generations. In this paper we present data indicating the

existence of genetic control of heat tolerance, and procedures for the evaluation of heat tolerance in parental lines and in the early generations of a breeding program. These procedures were used (a) to assess differences between various genotypes in their tuberization response under heat stress (high temperatures), and (b) for the selection of clones with improved tolerance to heat.

Materials and Methods

Evaluation of potato cultivars for heat tolerance

A wide range of genotypes of various maturity classes, was examined for the preliminary evaluation of heat tolerance (Table 1). Heat tolerance was evaluated under field conditions by planting tubers in the late spring (mid April) and growing the plants during the summer. Maximum day temperature and minimum night temperatures are given in Table 2. Daylength increased from 13 h on April 16 to 14 h 10 min on June 6. A five plant sample of each cultivar was taken on May 11 and May 26, 1982, and a seven plant sample on May 22, May 27, June 1 and June 6 in 1983. The number of stems, stolons, tuber initials (at least twice the thickness of the stolon), and tubers was recorded. At the last sampling date, the weight of tubers per plant was recorded. The plots were irrigated every other day to avoid drought stress.

Early maturing genotypes which form tubers and accomplish yield accumulation in a relatively short period of time, are likely to exhibit tolerance to heat in comparison to the late maturing genotypes which form

tubers and accomplish yield accumulation later and are exposed to the increasing temperatures for longer periods. Consequently, this situation could explain a relatively small yield loss of the early maturing genotypes (Levy, 1986b). To avoid this confounding effect, parameters of heat tolerance were recorded under controlled conditions. The relative performance in high vs. in cool temperatures, i.e., tubers per stem in the hot glasshouse divided by tubers per stem in the cool glasshouse was used to assess tolerance to heat.

Evaluation of heat tolerance in the glasshouse was done by planting tubers in trays filled with volcanic tuff. When most of the main stems had six or seven leaves and before the onset of tuberization, single main stems were replanted in tuff after recording the number of stolons. Ten to 15 single main stems of each cultivar were then placed in a glasshouse compartment set to 24-25°C during 12 h of the day and 15-16°C during the following 12 h (cool glasshouse); another group of 10-15 stems of each cultivar was placed in a second glasshouse compartment set to 32-34°C for 12 h of the day and to 20-21°C for the following 12 h (hot glasshouse). After 20 days, the plants were examined for the number of tubers and for tuber yield.

Based on the results of these experiments, cultivars which varied in tuberization under high temperatures and which also exhibited abundant flowering and reasonable fertility, were selected for further experiments including progeny tests. The cultivars chosen were Cara, Desiree and Blanka.

Evaluation of heat tolerance in progeny

Open pollinated (OP) true potato seed of cvs. Desiree, Cara, and Blanka and of crosses between the three cultivars were produced in a glasshouse or in net houses. Due to insufficient seed set of Blanka (OP) and the crosses Cara x Blanka and Desiree x Cara, these were not included in the progeny tests. The seeds were sown in speedling trays (Speedling Inc, Sun City, FL, U.S.A.) containing peat and vermiculite (2:1 vol/vol). The number of seedlings replicates and the growing conditions in the glasshouses are specified in Table 3. Irrigation was applied once or twice a day to avoid drought stress. The seedlings were examined periodically for tuberization by lifting each seedling gently and replanting it. Seedlings that developed tubers were transplanted in 10 cm² plastic pots in the cool glasshouse for further development.

After 88 days in the hot glasshouse, from each family, 50 of the seedlings which did not initiate tubers were transferred to the cool glasshouse under a photoperiod of 13 h to enhance tuberization. After 69 days, small tubers were harvested from the seedlings that formed tubers (Table 5). These tubers were placed in paper bags and kept at room temperature (18-23°C); they were examined periodically for sprouting, and with an apical sprout approximately 5 mm long were planted. This was done to diminish the effects of the physiological stage of the tuber on tuberization. The small tubers, 8-15 mm in diameter were planted in 10 cm² plastic pots containing peat and vermiculite and placed in the hot glasshouse (30-35°C for 13 h during the day, and 20-22°C during the night). The plants were examined periodically for tuberization as described earlier.

Statistical analysis of the results was conducted according to the Exact Fisher Test (Simmonds, 1981). In each family, the effects of temperature and daylength were assessed by comparing the results obtained in the hot glasshouse or under long days, with those obtained in the cool glasshouse with 13 h photoperiod, conditions that are considered to be optimal for tuberization (Borah and Milthorpe, 1962).

Results

Evaluation of parents

a) Field trials. In two field trials conducted during late spring and summer, the plants of 14 potato cultivars were exposed to increasing temperatures and daylength. Marked differences between the cultivars were observed in the timing of tuber initiation as well as in the rate of tuber formation (Fig. 1). Alpha and Kondor had no tuber initials on May 27, but more than 60% of the stems of Kondor had tubers whereas less than 10% of Alpha stems had tubers by June 6. On the other hand, Blanka had the highest percentage of tuber initials on May 27, and maintained a high percentage through June 6. Differences in the relative tuber yield per plant were also evident under these conditions (Fig. 2). Blanka followed by Diamant and Cleopatra, had high relative tuber yields, whereas the late-maturing cultivars, Cara and Alpha, had low tuber yields (Fig. 2). Accordingly, severe yield losses have been recorded in Cara and Alpha when grown in the hot summer, in comparison with the yields obtained in the spring season; however, in Desiree and especially in Blanka, yield losses have been less (Levy 1986a,b). These results indicated the relative

susceptibility of Alpha and Cara to heat stress, and the relative tolerance of Desiree and especially of Blanka to heat. However, inherent early tuberization (e.g., Blanka) vs. inherent late tuberization (e.g. Alpha) could lead to the differential yield losses of these genotypes. To avoid the confounding effect of the timing of tuberization, the relative inhibition of tuberization was assessed under controlled environment conditions in glasshouses.

b) Glasshouse experiments. The rate of tuber formation under favorable temperature conditions in the cool glasshouse is given in Table 4. In the early maturing cultivars, most of the stems had tubers after 20 days. The two late maturing cultivars Alpha and Cara were different with Cara forming tubers faster than Alpha in the cool glasshouse. The two very late maturing genotypes, LT7 and NT8, were the last to form tubers. In the hot glasshouse, tuberization was markedly inhibited except with Atica, in which the heat did not retard tuber formation but significantly reduced tuber growth. Again, there was a distinct difference between Cara-in which tuber formation was inhibited to a greater extent in the hot glasshouses-and Alpha, which, although slower in tuber formation, approached the earlier maturing cv. Desiree for stems with tubers in the hot glasshouse after 42 days. Severe inhibition of tuberization by heat was observed in the very late maturing genotypes LT7 and NT8. The confounding effect of earliness with tolerance to heat was avoided by expressing heat tolerance as the ratio between the performance in the hot glasshouse and the performance of the same cultivar in the cool glasshouse. This revealed that indeed earliness and tolerance to heat are associated (Fig. 3); however,

differential response to heat could be detected in cultivars of the same maturity class.

c) Evaluation of progeny. In seedling populations grown in the cool glasshouse under conditions favorable for tuberization, 11%, 27% and 37% of seedlings initiated tubers after 45 days in the progeny of Cara, Cara X Desiree, and Desiree, respectively (Fig. 4A). This is in accordance with the known tuberization behavior of the parents, Desiree being earlier than Cara (Levy 1986b).

As expected, long photoperiod generally retarded tuber initiation (Fig. 4B). However, in the progeny of the earlier tuberizing cultivar Desiree (i.e., which initiates tubers under longer photoperiod), the retardation of tuber initiation by the long days was less in comparison with the progeny of the late maturing cv. Cara, which favors a shorter photoperiod for tuber initiation (Ewing 1981). The retardation of tuber initiation in the progeny of Cara X Desiree was intermediate but closer to that obtained for progeny of the maternal parent Cara than in progeny of the male parent Desiree (Fig. 4B)

High temperatures strongly inhibited tuber initiation (Fig. 4C). In the progeny of Desiree and Cara X Desiree, 1.09% and 0.72 % of the seedling population, respectively, had visible tuber initials 58 days after emergence, while in the progeny of Cara, only 0.36% of the seedling population had tuber initials 75 days after emergence. Again, this is in accordance with the known response of the parents, Desiree being more capable of tuber initiation than Cara at high temperatures (Table 4). The

behavior of the Cara X Desiree population is interesting: tuber initials were visible concomitantly in the Cara X Desiree progeny and in the progeny of Desiree, indicating the prominent effect of the male parent. On the other hand, the rate of tuber initiation after 88 days in the Cara X Desiree progeny ($1.72 \pm 1.02\%$) was similar to that of the progeny of Cara ($1.42 \pm 0.97\%$), and both were lower than the tuberization rate of Desiree progeny ($3.92 \pm 1.13\%$). This resembles the behavior of the Cara X Desiree progeny at favorable temperature (Fig. 4A) and in long photoperiod (Fig. 4B). All three independent experiments (Fig. 4, A-C) indicate that in a seedling population of a hybrid, the control of timing of tuber initiation may be independent of the control of the rate of tuberization, and that each of these characters could be influenced by either parents. In the seedling population of Blanka X Cara, however, both timing and rate of tuber initiation differed greatly from the seedling population of Cara (Fig. 4C). Blanka is an early cultivar, earlier than Desiree, and is highly capable of tuber initiation at high temperatures (Fig. 1C). The differences in the timing of tuberization between the parents Blanka (early) and Cara (late) may have caused the departure of the tuberization timing and rate in their hybrid population (Blanka X Cara) from the seedling population of Cara (Fig. 4C).

Seedlings which did not form tubers in the hot glasshouse after 88 days, were transferred to the cool glasshouse and examined for tuber formation after an additional 69 days. Under the favorable temperature conditions 72%, 50% and 44% of the seedling progeny of Desiree, Cara X Desiree and Cara respectively, formed tubers (Table 5). These values were close to those obtained with seedlings which were not exposed to high temperatures

and examined 78 days after emergence (values in parentheses, Table 5), indicating that the inhibitory effect of high temperatures on tuber formation is reversible.

Tubers of the first clonal generation of Desiree progeny, harvested from seedlings grown in the hot glasshouse, had higher rates of tuber formation at high temperatures compared with tubers harvested from seedlings grown in the cool glasshouse (not selected for heat tolerance) (Fig. 5). Clones of Desiree progeny selected for tuber formation in the cool glasshouse under long days tuberized faster than those selected under short days at 40-50 days after planting in the hot glasshouse (Fig. 5), indicating that the inhibitory effect of long days on tuber initiation resembles, to a certain extent, that of the high temperatures. A similar trend was observed in the clonal progeny of Cara but not in the clones of Cara X Desiree (Fig. 5).

Tubers of the first clonal generation, harvested from seedlings which were first exposed to high temperature but formed tubers after their transfer to the cool glasshouse, had higher tuberization rates in Cara, in Cara X Desiree and to a lesser extent, also in Desiree, compared with the non-selected clones of the same families (Fig. 5). In Desiree and in Blanka X Cara, clones selected by pre-exposure to hot conditions followed by cool temperatures, were similar in their tuberization behavior to those selected in hot glasshouses (Fig. 5).

Discussion

The differential response of potatoes to high temperatures and the association of early maturation with tolerance to heat was clearly shown (Fig 3). Other observations of differences in the response to heat among cultivars (Ewing et al. 1987) and among potato species (Hawkes 1978; Reynolds and Ewing 1989) indicate that tolerance or susceptibility to heat is genetically controlled. The association of tolerance to heat with early maturity (Levy 1986b) indicates a possible linkage between genes controlling these attributes. However, early and late maturing cultivars might share a similar tuberization pattern under conditions favouring tuber formation (Table 4), indicating that genes controlling tuberization are strongly affected by the environment.

Screening seedling populations according to their capacity to tuberize in the hot glasshouse could lead to the loss of most of the seedling population due to the low percentage of tuberizing seedlings. Only the progeny of Blanka X Cara, where heat tolerance was greatly enhanced by the heat tolerant parent Blanka yielded sufficient selections under these conditions (Fig. 4C). The two-step selection procedure, i.e. exposure of seedlings to high temperatures followed by a growth period in cool temperatures, proved to be efficient for the selection of heat-tolerant clones; the seedlings of all genotypes responded well to the cool temperatures, and the percentage of tuberizing seedlings came close to that of seedlings which were not exposed to heat and formed tubers in the cool glasshouse (Table 5). However, these two groups were distinctly different, as demonstrated by the significant differences in the tuberization capacity

of the first generation clones in the hot glasshouse (Fig. 5). The reasons for this differential behavior are not clear. Although no specific selection was conducted upon the transfer of the seedlings from the hot to the cool glasshouse, it is probable that mostly well-developed and vigorous seedlings were transferred from the hot to the cool glasshouse. However seedlings grown only in the cool glasshouse were not subject to any type of selection. This two-step selection procedure, first at high temperatures followed by exposure to lower temperatures resembles the procedure described by Reynolds and Ewing (1989) who first assessed the vigor of shoot growth and later the ability to tuberize under high temperatures. As indicated by Ewing et al. (1987) and by Levy et al. (1986), it seems essential to have the proper balance between the capacity to form and enlarge the tuber and haulm growth, and the two-step selection procedure seems to accommodate this need.

This study showed that heat tolerance in *S. tuberosum* cultivars is associated with early maturity, controlled genetically and that heat-tolerant genotypes might be identified in the progeny of a heat susceptible parent. It was also shown that heat tolerance might be enhanced by crossing a heat tolerant cultivar such as Blanka, with a heat susceptible cultivar such as Cara (Table 5), and that the inheritance of the timing of tuber formation is independent of that of the rate of tuberization. The two-step screening procedure described in this study might be useful for the detection of heat tolerant clones (Fig. 5).

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Captions to figures

Figure 1. Tuber formation (percentage of stems with tubers) in potato cultivars of various maturity classes grown in the field in Bet Dagan under relatively high temperatures during the early summer season (1983). A- late, B- intermediate, C- early, and D- very early maturing cultivars. Bars represent the standard error (SE).

Figure 2. The relative tuber yields (yield of each of the cultivars/the mean of all 14 cultivars x 100) of potatoes grown in the summer seasons of 1982 (○) and 1983 (●). Mean yields were 44 and 70 g/plant in 1982 and 1983, respectively. AL, Alpha; BI, Bintje; BL, Blanka; CA, Cara; CL, Cleopatra; CO, Constante; DE, Desiree; DI, Diamant; GR, Gracia; KE, Kennebec; KO, Kondor; MO, Monalisa; MU, Murilo.

Figure 3. Tolerance to heat, estimated as the ratio of performance in the hot glasshouse to performance in the cool glasshouse, of: A- number of stems with tuber initials or tubers; B- number of tubers per stem; and C- yield of tubers per stem.

Figure 4. The effect of temperature and of daylength on tuberization of seedlings (percent of total population) grown from open pollinated seeds of Desiree (○) and Cara (Δ), and from hybrid seeds of Cara X Desiree (■) and Blanka X Cara (●). A- cool

glasshouse, 13 h photoperiod; B- cool glasshouse, 16 h photoperiod; C- hot glasshouse, 13 h photoperiod.

Figure 5. Tuberization in first-year clones (percent of total population) grown from small tubers in a hot glasshouse with a 13 h photoperiod. The tubers were harvested from seedlings grown under various conditions: cool glasshouse, 13 h photoperiod (o); cool glasshouse, 16 h photoperiod ($\square$); hot glasshouse 13 h photoperiod ($\blacktriangle$); 69 days in the cool glasshouse after 88 days in the hot glasshouse ($\bullet$), 13 h photoperiod in both. * = Significantly different ($P < 0.05$) in comparison with cool glasshouse and 13 h photoperiod treatment (O). (Exact Fisher Test, Simmonds 1981).

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Table 1. Cultivars and seed source of potatoes used in heat tolerance studies.

Maturity class	Cultivar	Seed Source
Very early	Arkula	Netherlands
	Bintje	Netherlands
	Cleopatra	Netherlands
	Constance	Netherlands
Early	Atica	FRG
	Blanka	Netherlands
	Gracia	Netherlands
	Monalisa	Netherlands
	Murillo	Netherlands
	Idit ^a	Israel
	Ori ^a	Israel
Intermediate	Kennebec	Netherlands
	Diamant	Netherlands
	Desiree	Netherlands
	Kondor	Netherlands
Late	Alpha	Netherlands
	Cara	Ireland
Very late	LT7 ^b	Israel
	NT8 ^c	Israel

^a Clones originated from open pollination of Desiree.

^b A clone introduced from the International Potato Center, Lima Peru.

^c A Neotuberosum clone.

Table 2. Daily mean maximum and minimum temperatures and the relative humidity prevailing during the experiments conducted in the field at Bet Dagan.

Month	<u>Daily mean temperatures (°C)</u>				<u>Relative humidity (%)</u>	
	Maximum		Minimum			
	<u>1982</u>	<u>1983</u>	<u>1982</u>	<u>1983</u>	<u>1982</u>	<u>1983</u>
April	25.3	22.0	12.4	10.3	63	68
May	26.1	26.2	13.4	13.4	61	65
June	28.7	28.7	15.4	16.7	63	64

Table 3

Environmental treatments and number of seedlings from which tuberizing selections were made from four potato families after 40, 50, 60, 70, and 80 days after planting. Cool glasshouse temperatures corresponded to 18-20° day, 15-16°C night; hot temperatures were 30-35°C day, 20-22°C night. Short days were 13 h, long days were 16 h. Daytime temperatures prevailed for 13 h regardless of photoperiod. D = Desiree (OP); C = Cara (OP); C x D = Cara x Desiree; B x C = Blanka x Cara.

Cool temperature, short day

D = 185

C = 185

C x D = 177

Cool temperature, long day

D = 173

C = 180

C x D = 178

Hot temperature, short day

D = 276

C = 275

C x D = 284

B x C = 295

**Two-step - Hot temp, short day for 88 days
followed by cool temp, short day for 69 days**

D = 50

C = 50

C x D = 50

B x C = 50

Table 4. The effect of temperature on tuberization 20 and 42 days after exposure to conditions in the cool (cool) vs hot (hot) glasshouse. SE= standard error.

Cultivar	Stems with tubers (%)				Tubers/stem+ SE				Tuber weight (g/stem +SE)			
	cool		hot		cool		hot		cool		hot	
	20	42	20	42	20	42	20	42	42	42	42	42
Atica	80	100	100	100	1.8+0.3	2.4+0.3	2.0+0.2	2.0+0.2	17.4+2.6	9.5+0.9		
Desirae	91	100	50	50	1.6+0.2	1.8+0.3	0.5+0.1	0.5+0.1	11.9+2.7	0.7+0.3		
Idit	100	100	60	60	2.7+0.3	2.4+0.3	0.6+0.1	0.9+0.2	8.8+1.1	0.6+0.2		
Ori	92	100	46	92	1.3+0.3	2.2+0.3	0.5+0.2	1.2+0.2	9.9+1.5	1.5+0.3		
Alpha	27	91	27	45	0.5+0.2	1.6+0.3	0.3+0.1	0.9+0.3	7.6+1.8	1.5+0.8		
Cara	87	100	20	20	1.7+0.3	2.0+0.2	0.2+0.1	0.2+0.1	10.9+1.1	0.02		
LT7	7	71	7	7	0.07	1.9+0.4	0.07	0.07	3.6+1.3	0.02		
NT8	0	81	0	0	0	2.2+0.7	0	0	3.1+1.0	0		

Table 5. Tuber formation in seedlings transferred to the cool glasshouse and grown there for 69 days after 88 days in the hot glasshouse without tuberization. For each family, 50 non-tuberizing seedlings were transferred. Values in parentheses are the percentage of seedlings that formed tubers in the cool glasshouse 70 days after emergence. OP= seeds obtained by open pollination.

Genotype	Seedlings with tubers (%)
Desiree (OP)	72 (82)
Cara (OP)	44 (61)
Cara X Desiree	50 (71)
Blanka X Cara	50 (-)

EVALUATION OF THE RESEARCH PROPOSAL WITH RESPECT TO THE ORIGINAL RESEARCH PROPOSAL

The original proposal included a request for \$498,275 U.S. to be used over a four year period. The rationale for this length of time was based upon the fact that breeding studies and implementation of genetic crosses requires several years of effort. The actual funding provided was \$190,000 to be used over a three year period. A revised budget was then submitted.

The shortened timeframe did not allow for a second round of genetic crosses or the final field evaluations. All other objectives have been completed. This includes the physiological studies with heat-tolerant and heat-susceptible genotypes, in particular studies of carbon uptake (photosynthesis), carbon loss (respiration) and carbon partitioning (translocation) under varied conditions of heat stress. These studies produced two Ph.D. dissertations, which have been completed and approved by the University of Idaho, and a separate paper on carbon partitioning (included with this report). One dissertation was concerned with photosynthesis of clones in response to heat stress, and the other with respiration in response to heat stress. Because of the interrelationship between these two processes, two of the chapters from each dissertation will be combined for submission to the research journals.

Evaluation of field screening methods has been completed in Israel. Several promising genotypes that have shown heat-tolerance under growth chamber conditions in Idaho have been sent to Israel for field screening. Rather than risking the spread of disease that could occur in sending tuber materials, we sent sterile stem cuttings in tissue culture via quarantine facilities in Israel. These clones will be multiplied and field tested in studies conducted subsequent to the three-year funding period. Reprints of all publications will be sent to BARD.

DESCRIPTION AND RESULTS OF COOPERATION

The Principal Investigator (R. Dwelle, USA) and the Cooperator (D. Levy, Israel) met and conferred on several occasions during the course of this project. R. Dwelle visited Israel for a week in April, 1987. This visit included consultation with research faculty and tours of research facilities and field sites. In July, 1987, Dwelle and Levy met at the Triennial Conference of the European Association for Potato Research, Aalborg, Denmark. At that time it was decided that rather than shipping a large quantity of true potato seed (TPS) from Idaho to Israel, which would be very cumbersome to pass through quarantine, instead the Principal Investigator would do a preliminary screening of the TPS and select only 10 or 12 clones, conduct DNA-hybridization tests for PSTV on these genotypes, and the pure clones would be shipped in vitro to the appropriate quarantine pathologist in Israel.

D. Levy visited Idaho for a week during July, 1988. At that time plans were finalized for the completion of the project. Dwelle and Levy met twice in 1989, in July at the annual conference of the Potato Association of America, Corvallis, Oregon, and in August at the Frist International Symposium on Molecular Biology of the Potato, Bar Harbor, Maine. The conclusion and final report for the project were planned at that time.

Through the cooperative efforts of this BARD project, we were able to meet objectives that could not have been achieved independently by the two laboratories. The Idaho portion of the program had experience and facilities for detailed physiological studies under controlled conditions in the glasshouse and growth chambers. The Israeli cooperator had the experience and appropriate climate to take the genetic materials to the field. The entire BARD project lead to a free exchange of ideas, methods and materials, and resulted in a better understanding of mutual interests and concerns.

LIST OF THESES

The Influence of High Temperatures on Photosynthesis and Dry Matter Distribution in Potato Clones. N. J. Malik, October, 1989. 96 pp.

The Influence of Temperature on Leaf Respiration and Relationship to Productivity of Potato Clones. M. K. Thornton, March, 1990. 86 pp.

The Influence of Heat Stress on Dry Matter Production and Photoassimilate Partitioning by Potato Plant. H. Gawronska, M. K. Thornton and R. B. Dwelle. 27 pp.