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BARD

**FINAL REPORT
PROJECT NO. US-2053-91**

Potato Germplasm Development for Warm Climates

R.E. Veilleux, D. Levy

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FOR POTATO RESEARCH

1996

45043

Date: 4/29/96

BARD Project Number: US-2053-91C

Project Title:

Potato germplasm development for warm climates

Investigators:
(Principal first)

Richard E. Veilleux

David Levy

Affiliated Institution:

Virginia Polytechnic Institute
and State University

A.R.O., The Volcani Center

Project Start Date: 10/1/92

Type of Report: 1st Annual _____ 2nd Annual _____ Final ✓

Richard E. Veilleux
Signature:
Principal Investigator

Signature:
Authorizing Official, Affiliated Institution

D. Levy

630.72
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BARD Final Scientific Report for Project No. US-2053-91C

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Abstract

Complex potato hybrids derived from crosses between cv. Atlantic and 11 clones of three genomic compositions, all with an unadapted component from previously identified heat tolerant accessions, were evaluated in the field in Israel and Virginia and in controlled environments in Israel. Heat tolerance was exhibited in the field by the ability of many of these hybrids to tuberize under severe heat stress when cv. Atlantic did not tuberize at all. The complex hybrids also exhibited fewer internal defects (heat necrosis, hollow heart) than Atlantic. Studies to determine if heat stress applied during anther culture or to pollen samples prior to pollination could affect gametic selection towards more heat tolerant progenies were also undertaken. There was some evidence of greater heat tolerance (longer survival under heat stress) in the anther-derived population that had been regenerated under heat stress. The seedlings resulting from crosses with heat-treated pollen also exhibited greater haulm growth under heat stress compared with controls. However, the poor adaptation of the germplasm prevented a firm conclusion about gametic selection. The introduction of exotic germplasm into cultivated potato has considerable potential to adapt potato to nontraditional growing seasons and climates. In a sample of 26 complex hybrids analyzed for glycoalkaloid levels, half of them had levels below the threshold generally considered safe for human consumption. However, such hybrids will require continued selection and evaluation to retain the traits required for commercial production.

Objectives of the original research proposal

Objective i: to identify $2n$ pollen producers with heat tolerance in order to develop $4x-2x$ hybrid families with a greater potential of heat tolerance.

Twenty diploid clones of complex hybrid origin were selected in Israel for heat tolerance by their ability to tuberize under heat stress (30°C 12 h/ 20°C 12 h) in a controlled environment. These clones represented four genomic compositions (APC, 15 clones; APB, 1 clone; AMPC, 3 clones; and P, 1 clone, where A = *S. andigena*, P = *S. phureja*, B = *S. berthaultii*, C = *S. chacoense* and M = *S. microdontum*). The 15 APC selections represented five different families. The clones were virus-tested and shipped to Virginia through the Israeli and USDA Plant Germplasm Quarantine Centers. In Virginia, the 20 clones were planted in the greenhouse as microtubers and pollen samples of the resulting 17 plants that survived were screened for the presence of $2n$ pollen. Ten plants had less than 1% $2n$ pollen, three had between 1 and 5% $2n$ pollen and four had greater than 10% $2n$ pollen. However, in crosses with cv. Atlantic, only two (RV22 and RV613) of the seven selections with greater than 1% $2n$ pollen resulted in fruit and seed set. RV22 was of the APC genomic composition whereas RV613 was *S. phureja*. The seed resulting from these crosses was virus-tested and sent to Israel through the USDA and Israeli Plant Germplasm Quarantine Centers.

A study of heat tolerance of $4x-2x$ hybrids was conducted in Israel where three of the $2x$ parents had been selected for heat tolerance and six other $2x$ parents were unselected for heat tolerance. The $4x-2x$ seedlings resulting from crosses of the two above selections (RV22 and RV613) with

Atlantic, a cross between another independently selected heat tolerant selection (BARD 10-2) and Atlantic, and seven crosses between Atlantic or Desiree and *S. phureja* (PP5, BARD 1-12), APC hybrids (APC3 and APC5), or AMPC hybrids {[$(1792 \times M2) \times PC15-77$] and [$(13030 \times M2) \times PC15-77$]} comprised the study. The ten families were examined for tuberization potential under 30-33°C day (12 h) and 20-22°C night temperatures. The number of seedlings evaluated per family varied from 30 to 106. Percent tuberization ranged from 0 to 47% (Table 1). Some heat tolerant seedlings were found in all of the progenies of cv. Desiree. However, only three of seven progenies of cv. Atlantic exhibited heat tolerant selections. Of the three $2n$ pollen producers that had been previously selected for heat tolerance (RV22, RV613, and BARD 10-2), only progeny of RV22 exhibited heat tolerance and these were at a lower frequency than progeny of some unselected diploids (e.g., APC3, Table 1). In the crosses with Atlantic, the genomic composition of the $2x$ parent was a better predictor of heat tolerant progeny than whether or not the $2x$ parent had been previously selected for heat tolerance. All three of the families in which heat tolerant progeny were identified in crosses with Atlantic resulted from crosses with diploids of the APC genomic composition whereas the other four progeny without heat tolerant individuals were the result of crosses with *S. phureja*. *S. chacoense* is a known source of heat tolerance whereas *S. phureja* is known to be generally heat sensitive. Selection for heat tolerance in the diploid $2n$ pollen producers appeared to have little effect on the expression of heat tolerance in the progeny.

Objective iia: to determine if heat stress applied during the androgenic process favors the development of embryos and subsequent plants more tolerant to heat.

Selection of androgenic clones

Ten complex hybrids, four APC, four APB, and two APM, that had previously been screened for $2n$ pollen production were screened for response to anther culture by culturing 10-14 flasks of 30 anthers according to standard procedures in Virginia. Three clones, one from each genomic composition, were found to respond to anther culture with a moderate yield of embryos whereas the other seven clones responded poorly or not at all (Table 2). These three clones were selected for additional anther culture experiments with heat treatments applied during culture.

Objective iib: to develop heat tolerant gametoclonal variants equivalent to clones unselected for heat tolerance from APC, APB, and APM hybrids.

Gametic selection resulting from heat treatments applied during anther culture

Heat treatments were applied during anther culture of clones APB3, APC3, and APM1, both as an initial heat shock of 35°C for 12 or 24 h or as elevated temperature (30°C day/20°C night) during the incubation period of five weeks. The control was cultured at 20°C continuously. These temperature treatments were applied to exert selection for heat tolerance during the androgenic process. However, an unexpected occurrence of elevated embryo production was observed for anthers given a 12 h heat shock followed by incubation at the elevated temperature. The experiment was repeated twice. The results were not always statistically significant but the trend was always the same (see Shen and Veilleux, 1995). The heat shock and elevated incubation temperature increased embryo production for all three clones. In vitro anther-derived plants that were regenerated after control and heat stress treatments during anther culture were virus-tested,

incubated on microtuberization medium for 10 weeks and the resulting microtubers were shipped to Israel through the USDA and Israeli Plant Germplasm Quarantine Centers.

Screen for heat tolerance of anther-derived diploids resulting from heat treated vs. control treatments during androgenesis

Of the 51 control and 54 heat treated microtubers shipped to Israel, only nine from control treatment and 13 from heat treatment (applied during androgenesis) germinated in Israel. The plants were planted pairwise, with four extra in the heat treatment group under 22°C day/18°C night for 10 days. The temperature was raised to 30-33°C day/20°C night and the days from planting to haulm drying were scored as an estimate of heat tolerance. Haulm drying of control plants occurred after 100 ± 3.6 days of heat treatment whereas that of the plants derived from heat treatment during anther culture was 113 ± 1.1 days. It would appear that there was some gametic selection towards more heat tolerant plants as a result of heat treatment during anther culture. However, the population size was too small to permit a definite conclusion. None of the plants formed tubers under heat stress.

Gametic selection resulting from heat treatments to pollen

Heat treatments of 0, 4, 12, and 24 h at 35°C were also applied to pollen collected from clone APB3 growing in the greenhouse in Virginia. The pollen samples were placed in Eppendorf microfuge tubes. After treatment, pollen viability was estimated by staining with fluorescein diacetate (FDA), filtering through a 75µM nylon mesh, and analyzing with an Epics V, Model 752 laser flow cytometer. Although pollen appeared to be viable after 24 h treatment, no seed set resulted when it was used to pollinate receptive stigmas of the doubled monoploid clone, AD2-4.

Only when the treatment was reduced to 4 h at 35°C did fruit set occur. Pollinations were done pairwise such that a control pollination and a pollination with heat-treated pollen were done on adjacent flowers on an inflorescence. Three pairs of fruit were collected. The seed was extracted, virus-tested and shipped to Israel for estimation of heat tolerance that may have resulted from gametic selection.

Screen for heat tolerance of seedlings resulting from heat treated vs. control pollen in Israel

Three pairs of seed lots, P1C/P1H, P2C/P2H, and P3C/P3H, were received from Virginia where the C and H in the designation refer to seeds resulting from pollination of doubled monoploid clone AD2-4 with control or heat-treated (35°C for 4 h) pollen of APB3. The homozygous doubled monoploid clone had been selected as the female parent because of the expected homogeneity of its gametes; most of the variation among the progeny should have resulted from genetic segregation in the highly heterozygous pollinator. We hoped to determine if the heat treatment applied to the pollen affected this segregation. The number of seeds varied from 18 to 188 per lot. Germination rate ranged from 42 to 81%. The germination rate was always lower for the seeds resulting from the heat-treated pollen (Table 3). After 27 days at 18/22°C, the seedlings were planted pairwise in three replications, ten pairs per replication, to assess their performance under heat stress (30°C 12h/20°C 12 h) in a controlled environment. Haulm weight, node number, and stem length were measured 80 days after the heat treatment was started.

There were no significant treatment effects associated with the heat treatment to pollen. The mean haulm weight was greater for the plants resulting from the heat treatment (mean = 65 and 56 g/plant, respectively) for all three pairs (Table 3), but the standard error was too great to permit

statistical separation. Node number (35 for both treatments) and stem length (112 cm for heat treatment, 108 cm for control) exhibited little difference between treatments (Table 3). Only a single plant tuberized (in the control treatment), permitting no conclusion about the effect of heat treated pollen on gametic selection for tuberization under heat stress. The poor adaptation of the interspecific hybrids may have limited their ability to tuberize under conditions where heat tolerant selections would be expected to tuberize.

Objective iii: to determine if the genomic composition of 4x-2x hybrids affects their performance under heat stress.

Hybrids between *S. tuberosum* cv. Atlantic and 11 2n pollen-producing clones of three genomic compositions (APB -- 4 families; APC -- 4 families; and APM -- 3 families, where A = *S. andigena*, P = *S. phureja*, C = *S. chacoense*, B = *S. berthaultii* and M = *S. microdontum*) were examined under field conditions in both Israel and Virginia.

Screen for heat tolerance among complex 4x-2x hybrids under heat stress in Israel

Seed of the 11 complex potato hybrid families (Table 4) developed in Virginia (BARD US-1196-86 final report, 1991) were virus-tested and shipped to Israel through the USDA and Israeli Plant Germplasm Quarantine Centers. The seedlings were used in controlled experiments under four temperature regimes (22/12°C, 28/18°C, 30/20°C and 25-40/20°C, day/night, 12 h photoperiod) to determine if the frequency of tuberization under heat stress was dependent upon the genomic composition of the hybrids. During the day, supplementary light was provided by a SON/T400 lamp equipped with a SGR reflector (Phillips, The Netherlands).

For the studies under controlled environment, 30 seedlings of each family were grown under each temperature regime in 400 ml pots in Solit Potting mix (Solit, Israel) containing slow release fertilizer. The seedlings were frequently irrigated by overhead mini-sprinklers to avoid water deficiency. Once weekly, a composite fertilizer solution containing N, P_2O_5 , K_2O and microelements of a progressive rate of 100-200 ppm N was applied in the irrigation water.

Heat screen under controlled environment revealed that tuberization was generally better under 28/18°C than under 22/12°C which is considered optimal for tuberization of potato (Table 5). The percent of seedlings with tubers, tuber number per seedling, tuber yield per plant, and average tuber weight were all greater at 28/12°C than at 22/12°C. The higher temperatures (30/20°C, 25-40/20°C) slightly reduced the percent tuberization but in some families there was little effect on the number of tubers per seedling. However, in all families the high temperatures diminished tuber weight per plant and inhibited tuber growth (Table 6). This demonstrated that, in these genomic compositions, high temperatures significantly reduced the processes eventually associated with tuber growth, e.g., photosynthate accumulation in the tubers and tuber enlargement, while the morphogenic processes associated with tuber initiation were practically unaffected. This illustrated that two of the components involved in heat tolerance in potato, i.e., tuber initiation and tuber enlargement are independent of each other. The differential capacity of tuber enlargement among the families indicates some genetic control of this attribute. It is noteworthy that, in *S. tuberosum* cultivars as well as in seedling progeny of *S. tuberosum* cultivars, high temperatures have strongly retarded both tuber initiation and tuber growth. The present data demonstrate the possibility to enhance heat tolerance by diminishing the adverse effect of high temperature on tuber initiation using other potato germplasm. Families 101 (TAPB) and 105

(TAPC) seemed to maintain better tuberization capacity and tuber growth under heat stress compared to the other families (Table 6).

After harvest, the tubers from the various temperature regimes of all 11 families were stored at room temperature (20-25°C) in paper bags. After three months most of the tubers had sprouted (Table 7). Tubers grown at 28/18°C were more fully sprouted than those grown at 22/12°C. The shelf life of the tubers, assessed by tuber shrivelling was influenced by the temperature at which tubers were grown, some of the families showed greater susceptibility than others, and one family (101) was tolerant (Table 7).

A second experiment was conducted to examine the stability of heat tolerance in the same germplasm propagated vegetatively instead of from seed. Fully sprouted small tubers (15-33 mm diam) were planted in the hot glasshouse (30/20°C, day/night). After 81 days, the temperature was decreased to allow tuber enlargement. No differences were noticed in tuber formation or tuber number per plant (Table 8) reflecting the results obtained with seedlings (Tables 5, 6). However, unlike the experiment with seedlings, no differences were observed for tuber weight per plant among the groups of clones within each family previously grown at the different temperature regimes (Table 8). It is worth noting that in first year clones of *S. tuberosum* progenies, the temperature at which the seedlings have been selected influenced their subsequent behavior on exposure to high temperature. This emphasizes the differential behavior of the genomic compositions developed in this study in their tolerance to high temperature. Hence, an additional test was conducted in a hot glasshouse with day temperatures of 32-38°C (12 h) and night temperatures of 20-23°C, which were higher than temperatures used in previous studies. Clones

selected at the higher temperatures survived better at the extreme heat and some managed to form tubers compared to those selected at the lower temperatures (Table 9).

Tubers generated under controlled environment were harvested and stored for at least three months before planting in the field to determine the frequency of tuberization at flowering under naturally occurring heat stress. The field experiments were carried out at the Volcani Center, Experiment Station, Bet Dagan, located in the coastal plain of Israel. The climate is subtropical Mediterranean: the average winter rainfall (October to March) is 520 mm and the relevant climatological data are shown in Table 10. The soil is a typical light loam (chromic luvisols) uniform to a depth of 90 cm, with a field capacity of about 13%. The plots for the field experiments were treated with methyl bromide (40 kg/0.1 ha), in the autumn. Four tons/0.1 ha compost were dispersed in the area and the fertilizers superphosphate, ammonium sulphate and potassium chloride (Fertilizers & Chemicals Ltd., Israel) were applied at a rate of 80, 60 and 40 kg/0.1 ha, respectively. Liquid fertilizer (Nutricol) was added through the sprinkler irrigation system at the concentration of 10 l/0.1 ha every 15 days, from day 30 of growth until 30 days before harvest. The fields were irrigated twice a week according to Class A pan evaporation.

Due to limited number of tubers, the clones selected under 22/12°C and 28/18°C day/night treatments were planted on April 1 (late spring) and those selected under 30/20°C and 40/20°C were planted on April 29 to evaluate growth under the severe summer heat of June-July (Table 11). The plants were individually harvested at the physiological stage of first flowering and tubers numbers and weight were recorded. The mild early summer (April 1 planting) did not have much effect on tuber formation. Tuber numbers per plant were greater for the hybrids than for Atlantic,

the female parent of all the hybrids, but tuber yields were lower. However, exposure of the clones to the severe summer conditions (April 29 planting) diminished tuber formation and yield for all plants. Atlantic produced no tubers at all. Other *S. tuberosum* cultivars planted for comparison produced only a few small tubers. Blanka was the most productive cultivar but family 111 (TAPM) was the most heat tolerant under these field conditions. Although clones within the family shared many attributes, mainly tuber shape and skin color, there were noticeable differences among clones in appearance and other tuber qualities. Selected clones were assessed for the accumulation of glycoalkaloids in the tubers, since glycoalkaloid levels may be elevated in this germplasm.

Longitudinal quarters of 10 tubers were sampled for TGA (total glycoalkaloids) extracted according to Van Gelder's colorimetric method. TGA was determined colorimetrically 30 min after the addition of 10 ml freshly prepared Clarke reagent (300 ml paraformaldehyde l⁻¹ H₃PO₄ 85%) to 1 ml H₃PO₄ solution with tuber precipitate, at the wavelength of 66 nm in a spectrophotometer (Spectronic, Bausch & Lomb, USA).

Many of the 2x male parents contained high levels of glycoalkaloids. In addition, biotic and abiotic stresses tend to enhance alkaloid metabolism. In earlier studies in Israel, elevated levels of glycoalkaloids were measured in tubers exposed to high temperatures. Glycoalkaloid levels higher than 20 mg/100 g tuber fresh weight are considered unsafe for human consumption. Half of the complex hybrid selections grown in the summer season fell into the unacceptable category (Table 12). However, heat tolerance was not necessarily associated with high glycoalkaloid levels. The tubers in this study were generally small and small tubers tend to express higher levels of

glycoalkaloids. Based on previous experience, it can be predicted that marketable sized tubers of these same clones would express lower glycoalkaloid levels.

Performance of complex 4x-2x hybrids under heat stress in Virginia

In Virginia, 100 seeds of each of the 11 complex hybrid families were planted in August, 1992 and resulting seedlings were transplanted into 10 cm plastic pots. The seedlings were grown under natural light in the greenhouse for four months. In December, 1992, the seedlings tubers were harvested and stored at 4°C for approx. three months. The greenhouse tubers were then used to plant a replicated field plot on April 23, 1993. The field plot consisted of 11 families (representing three genomic compositions) and the cultivar check, Atlantic. Each plot consisted of 15 plants and the experiment was replicated three times.

Data were collected on days to shoot emergence, days to flowering, tuber yield per plant at harvest (Sept. 13, 1993), tuber set per plant, and frequency of three internal defects -- hollow heart, heat necrosis, and second growth -- determined on six randomly selected tubers per plant at harvest.

The season was especially hot resulting in a good assessment of heat tolerance under natural heat stress conditions. Regardless of genomic composition, all of the seedlings grown from greenhouse tubers in the field were later to emerge and later to flower than cv. Atlantic (Table 13). The total tuber yield of plants in genomic compositions TAPC and TAPM did not differ significantly from that of Atlantic whereas that of plants in genomic composition TAPB was significantly lower (Table 14). Tuber set was higher for all of the complex hybrids compared to Atlantic, resulting in

smaller average tuber weight for the hybrids. The frequency of tubers with hollow heart was significantly less for genomic compositions TAPB and TAPM compared to Atlantic and TAPC (Table 15). The frequency of tubers with heat necrosis was less for all of the complex hybrids compared to Atlantic; however, second growth was more common for the complex hybrids, especially TAPC and TAPM compared to Atlantic (Table 15).

Relevant data

Table 1. The percent of seedlings bearing tubers (tuberization), the number of tubers and the average tuber yield (g) per seedling of TPS derived seedlings grown in a greenhouse and exposed most of the day (12h) to temperatures of 30-33°C and night temperatures of 20-22°C for 79 days.

Family	Number of seedlings	Tuberization (%)	Tubers/ seedling	Tuber yield/seedling (g)
ATL × PP5	54	0	-	-
ATL × APC3	87	47	2.5 ± 0.2	6.3 ± 1.0
ATL × APC5	91	31	2.3 ± 0.3	2.6 ± 0.8
ATL × 1-12	30	0	-	-
ATL × 10-2*	54	0	-	-
ATL × RV22*	53	11	3.7 ± 0.9	8.0 ± 2.6
ATL × RV613*	86	0	-	-
DES × 1-12	78	3	2.0 ± 1.0	7.5 ± 4.3
DES×(1792×M2) × PC15-77]	79	20	1.6 ± 0.2	2.3 ± 0.7
DES×[(13030×M2) × PC15-77]	106	7	2.7 ± 1.1	2.6 ± 0.7

* Identified as HT.

Table 2. Response to anther culture of ten complex potato hybrids.

Clone*	No. of anthers cultured	No. of embryos	Embryos per anther
APB1	300	0	0
APB2	420	0	0
APB3	360	150	0.42
APB4	390	1	0.003
APC2	360	0	0
APC3	390	26	0.07
APC4	360	3	0.008
APC5	420	0	0
APM1	360	114	0.32
APM2	360	11	0.03

A = *S. andigena*, P = *S. phureja*, C = *S. chacoense*, B = *S. berthaultii*, M = *S. microdontum*

Table 3. Seed germination and characteristics of plants of families resulting from crosses between homozygous doubled monoploid clone AD2-4 and control (P1C, P2C, P3C) or heat-treated (P1H, P2H, P3H) pollen of the heterozygous interspecific hybrid APB3. The data were taken after the plants had been growing for 80 days under heat stress in a controlled environment.

Seed lot	No. of seed sown	Percent germination	Haulm wt. (g)	No. of nodes	Stem length (cm)
P1C	75	70	56	35	108
P1H	45	69	71	35	111
P2C	188	81	62	36	117
P2H	84	69	64	35	113
P3C	18	61	37	32	73
P3H	33	42	58	33	107

Table 4. The genomic compositions obtained from crosses between *Solanum tuberosum* (T) cv.Atlantic and the diploid hybrids: APB [*adg* × (*phu* × *ber*)]; APC [*adg* × (*phu* × *chc*)];APM [*adg* × (*phu* × *mcd*)].

Genomic composition	Male	Family number
TAPB	APB-1	101
	APB-2	102
	APB-3	103
	APB-4	104
TAPC	APC-2	105
	APC-3	106
	APC-4	107
	APC-5	108
TAPM	APM-1	109
	APM-2	110
	APM-5	111

Table 5. The effect of temperature on tuberization (%) on the number and weight of tubers per seedling, and on the percent of seedlings in each family ($\pm$ standard error) which were able to produce yields of 25-50 g/plant, of 50-100 g/plant and >100 g/plant. Harvested 95 days after sowing.

Family	Seedling		Tubers/scedling		Tuber weight (g/plant)	Seedlings with 25-50 g/plant		Seedlings with 50-100 g/plant		Seedlings with> 100	
	Number	% with tubers	>20 mm	Total		Percent	Mean weight	Percent	Mean weight	Percent	Mean weight
Day temperature 22°C (12 h) night temperature 12°C											
101	30	100	1.5±0.1	2.6±0.2	23±1	27	33±3	0		0	
102	30	90	1.2±0.2	3.0±0.3	19±2	20	30±1	0		0	
103	30	100	1.4±0.2	4.1±0.3	22±1	33	31±2	0		0	
104	30	97	1.1±0.1	3.4±0.4	19±1	13	32±2	0		0	
105	30	100	1.4±0.2	2.5±0.2	19±1	20	29±2	0		0	
106	30	100	1.2±0.1	3.1±0.4	20±1	17	30±3	0		0	
107	30	93	1.1±0.1	2.7±0.3	20±2	27	31±2	0		0	
108	17	77	1.3±0.3	3.8±0.4	23±2	35	28±1	0		0	
109	30	43	1.5±0.4	4.1±0.5	21±3	13	33±3	0		0	
110	30	100	1.4±0.2	3.4±0.3	23±2	43	32±2	0		0	
111	30	100	1.4±0.2	3.1±0.2	21±1	27	32±1	0		0	
Day temperature 28°C (12 h) night temperature 18°C											
101	30	100	3.3±0.3	5.3±0.4	59±6	0		33	71±6	17	116±4
102	30	47	2.6±0.3	4.2±0.6	44±7	0		13	62±4	3	100
103	30	97	2.1±0.1	4.2±0.4	30±3	0		10	73±11	0	
104	30	100	2.9±0.2	4.8±0.3	39±3	50	36±2	27	64±3	0	
105	15	100	2.1±0.4	4.4±0.4	42±5	40	35±3	40	63±3	0	
106	15	100	2.8±0.2	4.4±0.5	45±6	47	36±3	33	73±9	0	
107	15	100	2.2±0.2	3.1±0.4	38±6	53	38±2	20	71±9	0	
108	15	60	3.6±0.4	5.3±0.6	56±9	13	44±3	33	74±7	0	
109	15	60	2.6±0.2	4.4±0.5	42±3	40	41±2	13	54±2	0	
110	15	100	2.3±0.3	3.8±0.5	40±6	67	35±2	13	56±4	0	
111	15	100	2.5±0.3	5.0±0.5	40±4	60	41±2	20	59±7	0	

Table 6. The effect of temperature on tuberization (%), on the number and weight of tubers per seedling, and on the percent of seedlings in each family ($\pm$ standard error) which were able to produce yields of 25-50 g/plant, of 50-100 g/plant and of >100 g/plant. Harvested 95 days after sowing. The high temperature treatments started 15 days after sowing and lasted for 61 days.

Family	Seedling		Tubers/seedling		Tuber weight (g/plant)	Seedlings with 25-50 g/plant		Seedlings with 50-100 g/plant		Seedlings with>100	
	Number	% with tubers	>20 mm	Total		Percent	Mean weight	Percent	Mean weight	Percent	Mean weight
Day temperature 30°C (12 h) night temperature 20°C											
101	30	97	0.9±0.2	3.0±0.3	13±2	10	29±2	0	29±2	0	0
102	30	53	1.3±0.3	3.6±0.5	18±3	13	35±2	0	35±2	0	0
103	30	57	0.7±0.2	2.9±0.4	8±2	3	34	0	34	0	0
104	30	89	0.9±0.2	3.2±0.3	11±1	3	26	0	26	0	0
105	30	83	0.9±0.2	4.5±0.4	15±2	10	29±2	0	29±2	0	0
106	30	83	1.2±0.1	3.2±0.3	16±2	17	28±1	0	28±1	0	0
107	30	83	0.6±0.1	2.2±0.2	10±2	7	28±2	0	28±2	0	0
108	30	40	0.5±0.2	2.4±0.4	7±2	0	0	0	0	0	0
109	30	53	0.6±0.2	2.9±0.3	8±2	0	0	0	0	0	0
110	30	33	0.6±0.3	2.8±0.5	9±3	3	25	0	25	0	0
111	30	57	0.6±0.2	2.8±0.4	9±1	0	0	0	0	0	0
Day temperature 25 - 40°C (12 h) night temperature 15 - 20°C											
101	30	97	2.3±0.3	4.2±0.5	18±2	30	30±1	0	30±1	0	0
102	30	57	1.4±0.2	2.9±0.4	12±2	3	30	0	30	0	0
103	30	80	1.0±0.2	3.3±0.4	12±2	3	32	0	32	0	0
104	30	90	1.5±0.3	4.9±0.6	16±2	17	29±3	0	29±3	0	0
105	30	97	1.6±0.3	4.6±0.4	21±2	33	33±3	0	33±3	0	0
106	30	93	1.4±0.2	2.6±0.3	12±1	7	27±1	0	27±1	0	0
107	30	83	1.3±0.1	2.5±0.2	13±1	3	29	0	29	0	0
108	30	60	1.8±0.3	2.3±0.6	19±2	13	33±3	0	33±3	0	0
109	30	30	1.1±0.3	3.1±0.7	11±2	0	0	0	0	0	0
110	30	90	1.1±0.2	3.6±0.4	13±2	7	35±7	0	35±7	0	0
111	30	77	1.0±0.2	3.5±0.3	12±2	10	31±3	0	31±3	0	0

Table 7. The percent of sprouting (over half the tubers with a white sprout initial of ca 2 mm) and the percent of clones with at least one dry tuber (a tuber which lost turgor and shrivelled) after 3 months of storage in paper bags in room temperature (20-25°C). The tubers were grown in 4 different temperature regimes:

Temperature regime during growth (daytime/night temperature)												
22/12°C				28/18°C				30/20°C				
Family	Number of clones	Sprouting Clones (%)	Clones having dry tubers (%)	Number of Clones	Sprouting Clones (%)	Clones with dry tubers (%)	Number of Clones	Sprouting Clones (%)	Clones with dry tubers (%)	Number of Clones	Sprouting Clones (%)	Clones with dry tubers (%)
101	30	93	0	30	100	0	30	100	0	29	93	0
102	27	78	7	14	100	0	16	100	1	17	76	18
103	30	93	0	29	100	7	17	100	6	24	92	4
104	29	90	0	30	100	3	26	100	4	27	89	0
105	30	93	0	15	100	13	25	96	4	29	76	14
106	30	63	0	15	93	0	25	88	0	28	96	4
107	28	75	0	15	100	0	25	57	0	25	80	12
108	13	100	0	9	100	22	12	92	17	18	94	6
109	13	85	0	9	100	11	16	100	13	9	89	11
110	30	97	0	15	100	0	10	100	20	27	96	11
111	30	97	0	15	100	0	17	100	0	23	96	4

Table 8. The effect of temperature (30°C day, 20°C night) started 5 days after planting on tuberization (yield $\pm$ standard error) of clones of 11 families which were previously selected from true potato seed under various temperature conditions (treatments) (day/night temperatures, see Materials and Methods). Harvested 111 days after planting.

Family	Treatment	Number of clones (plants)	Clones with tubers (%) after			Yield after 96 days*	
			37 days	56 days	96 days	Tubers/plant	Weight/plant (g)
101	22/12°C	30	3	17	79	2.3 $\pm$ 0.2	17.6 $\pm$ 2.2
	28/18°C	30	0	7	100	2.9 $\pm$ 0.3	39.0 $\pm$ 2.1
	30/20°C	30	4	14	77	3.3 $\pm$ 0.4	25.7 $\pm$ 3.8
	40/20°C	29	15	19	66	2.4 $\pm$ 0.3	26.0 $\pm$ 4.6
102	22/12°C	27	0	4	56	2.1 $\pm$ 0.3	24.7 $\pm$ 5.7
	28/18°C	14	0	0	89	2.1 $\pm$ 0.2	15.4 $\pm$ 2.2
	30/20°C	16	0	0	73	1.3 $\pm$ 0.2	12.9 $\pm$ 2.1
	40/20°C	17	0	8	65	2.4 $\pm$ 0.3	40.1 $\pm$ 9.3
103	22/12°C	30	0	0	47	2.6 $\pm$ 0.4	16.0 $\pm$ 2.8
	28/18°C	28	0	0	89	1.9 $\pm$ 0.4	22.1 $\pm$ 2.7
	30/20°C	24	4	4	76	3.6 $\pm$ 0.3	25.5 $\pm$ 4.7
	40/20°C	29	0	4	58	2.2 $\pm$ 0.3	18.7 $\pm$ 3.6
104	22/12°C	29	3	10	69	2.9 $\pm$ 0.3	28.5 $\pm$ 3.9
	28/18°C	30	0	0	47	3.0 $\pm$ 1.0	45.4 $\pm$ 10.5
	30/20°C	26	4	24	72	3.8 $\pm$ 0.5	34.0 $\pm$ 6.0
	40/20°C	27	4	12	81	3.8 $\pm$ 0.3	40.2 $\pm$ 6.2
105	22/12°C	30	10	3	87	2.5 $\pm$ 0.3	26.4 $\pm$ 5.0
	28/18°C	15	0	0	67	3.5 $\pm$ 0.5	34.1 $\pm$ 7.7
	30/20°C	25	9	13	84	3.0 $\pm$ 0.2	29.1 $\pm$ 5.1
	40/20°C	29	0	7	76	3.3 $\pm$ 0.4	36.0 $\pm$ 4.2
106	22/12°C	30	3	3	60	2.9 $\pm$ 0.5	25.5 $\pm$ 3.2
	28/18°C	15	0	7	87	3.3 $\pm$ 0.2	40.7 $\pm$ 4.6
	30/20°C	25	8	12	60	2.3 $\pm$ 0.3	22.5 $\pm$ 4.0
	40/20°C	28	0	9	69	2.7 $\pm$ 0.4	28.1 $\pm$ 5.4
107	22/12°C	28	0	26	72	2.0 $\pm$ 0.2	26.0 $\pm$ 4.6
	28/18°C	15	0	6	86	3.1 $\pm$ 0.5	39.4 $\pm$ 7.2
	30/20°C	25	13	17	68	2.2 $\pm$ 0.3	24.2 $\pm$ 2.8
	40/20°C	25	0	0	80	1.7 $\pm$ 0.3	25.2 $\pm$ 3.0
108	22/12°C	13	9	9	100	2.7 $\pm$ 0.5	26.0 $\pm$ 3.7
	28/18°C	9	0	0	72	3.6 $\pm$ 0.3	36.4 $\pm$ 6.0
	30/20°C	12	0	0	75	2.2 $\pm$ 0.3	17.8 $\pm$ 2.8
	40/20°C	18	0	0	89	3.2 $\pm$ 0.4	32.9 $\pm$ 6.8
109	22/12°C	13	0	8	67	2.9 $\pm$ 0.7	20.1 $\pm$ 4.8
	28/18°C	9	0	0	93	2.7 $\pm$ 0.3	20.8 $\pm$ 3.2
	30/20°C	16	0	0	44	2.2 $\pm$ 0.4	22.0 $\pm$ 4.9
	40/20°C	9	0	0	33	2.0 $\pm$ 0.6	23.0 $\pm$ 9.9
110	22/12°C	30	0	3	63	1.8 $\pm$ 0.2	18.9 $\pm$ 3.0
	28/18°C	15	0	0	80	2.2 $\pm$ 0.4	16.5 $\pm$ 2.2
	30/20°C	10	10	10	50	2.0 $\pm$ 0.3	28.8 $\pm$ 6.0
	40/20°C	27	0	4	67	2.0 $\pm$ 0.2	20.6 $\pm$ 3.3
111	22/12°C	30	7	10	70	2.7 $\pm$ 0.3	21.5 $\pm$ 3.1
	28/18°C	15	0	7	60	3.2 $\pm$ 0.6	37.0 $\pm$ 7.5
	30/20°C	17	24	24	65	2.4 $\pm$ 0.5	23.1 $\pm$ 4.8
	40/20°C	23	5	5	74	3.9 $\pm$ 0.4	39.0 $\pm$ 5.0

* During the last 30 days, the temperature was 23°C during the day (12 h) and 16°C during the night.

Table 9. Survival and tuberization (percent of plants that initiated tubers) at day temperatures of 32-38°C (12 h) and night temperatures of 20-23°C. First clonal generation tubers of the family 104 (15-30 mm in diameter) were grown for 120 days.

Temperature at which the clones were selected	Number of tubers planted	Survival after 80 days (%)	Tuberization (%)
22/12°C	19	2.4	0
28/18°C	19	10.8	15.8
30/20°C	12	16.6	16.6
25-40/20°C	5	20.0	0

Table 10. Daily mean maximum and minimum temperatures and relative humidity prevailing during the experiments conducted in the field (1994) at Bet Dagan.

Month	Daily mean temperature (°C)		Relative ¹ humidity (%)
	maximum	minimum	
April	26.6	13.5	43.0
May	27.3	15.5	46.0
June	29.3	18.7	49.0
July	30.5	21.0	56.0

¹ At 14.00 hr.

Table 11. Tubalization and yield components ($\pm$ standard error) of clones of 11 families and 6 cultivars grown in late spring and in the summer in the field.

Family or cultivar	Minitubers produced at day/night temperatures ($^{\circ}$ C)	Date planted in the field	Number of clones planted	Days till harvest	Clones which formed tubers (%)	Tubers/plant	Tuber weight (g/plant)
101	22/12 28/18	April 1	25	47 $\pm$ 0.5	92	8.8 $\pm$ 1.6	58 $\pm$ 12
	30/20	April 1	27	47 $\pm$ 0.5	87	7.1 $\pm$ 1.1	47 $\pm$ 10
	25-40/20	April 29	25	46 $\pm$ 1.7	40	1.3 $\pm$ 0.4	5 $\pm$ 2
102	22/12	April 29	25	45 $\pm$ 1.7	68	1.3 $\pm$ 0.4	19 $\pm$ 11
	28/18	April 1	23	48 $\pm$ 0.5	87	6.7 $\pm$ 1.5	29 $\pm$ 10
	30/20	April 1	11	44 $\pm$ 0.8	100	5.7 $\pm$ 0.8	35 $\pm$ 10
103	25-40/20	April 29	-	-	-	-	-
	22/12	April 29	11	47 $\pm$ 2.0	64	1.2 $\pm$ 0.5	39 $\pm$ 21
	28/18	April 1	29	48 $\pm$ 0.5	69	6.8 $\pm$ 1.6	43 $\pm$ 11
	30/20	April 1	24	47 $\pm$ 0.5	92	11.6 $\pm$ 1.7	71 $\pm$ 15
	25-40/20	April 29	14	53 $\pm$ 2.0	43	1.0 $\pm$ 0.5	4 $\pm$ 3
104	22/12	April 29	22	47 $\pm$ 1.5	32	0.9 $\pm$ 0.5	16 $\pm$ 13
	28/18	April 1	26	49 $\pm$ 0.8	92	9.0 $\pm$ 1.9	109 $\pm$ 28
	30/20	April 1	29	50 $\pm$ 0.5	97	12.7 $\pm$ 1.8	137 $\pm$ 24
	25-40/20	April 29	23	50 $\pm$ 2.0	61	2.8 $\pm$ 0.8	45 $\pm$ 17
105	22/12	April 29	26	47 $\pm$ 1.7	62	2.2 $\pm$ 0.6	46 $\pm$ 19
	28/18	April 1	24	47 $\pm$ 0.7	96	12.2 $\pm$ 2.0	103 $\pm$ 29
	30/20	April 1	10	47 $\pm$ 1.6	90	11.0 $\pm$ 2.8	61 $\pm$ 25
	25-40/20	April 29	23	44 $\pm$ 1.5	35	1.3 $\pm$ 0.5	22 $\pm$ 14
106	22/12	April 29	24	40 $\pm$ 0.7	79	2.2 $\pm$ 0.5	30 $\pm$ 20
	28/18	April 1	26	48 $\pm$ 0.5	85	7.1 $\pm$ 1.4	47 $\pm$ 13
	30/20	April 1	14	46 $\pm$ 0.7	100	8.5 $\pm$ 1.6	58 $\pm$ 16
	25-40/20	April 29	21	44 $\pm$ 1.3	52	2.0 $\pm$ 0.7	3 $\pm$ 1
107	22/12	April 29	20	43 $\pm$ 2.1	65	2.0 $\pm$ 0.5	22 $\pm$ 17
	28/18	April 1	26	49 $\pm$ 0.6	100	9.4 $\pm$ 1.1	95 $\pm$ 17
	30/20	April 1	14	47 $\pm$ 0.9	93	9.3 $\pm$ 1.9	98 $\pm$ 33
	25-40/20	April 29	6	45 $\pm$ 2.2	80	0.8 $\pm$ 0.4	5 $\pm$ 3
108	22/12	April 29	16	42 $\pm$ 1.4	75	1.5 $\pm$ 0.3	4 $\pm$ 1
	28/18	April 1	12	48 $\pm$ 0.8	100	13.4 $\pm$ 1.7	91 $\pm$ 17
	30/20	April 1	8	48 $\pm$ 1.1	88	12.5 $\pm$ 4.3	79 $\pm$ 34
	25-40/20	April 29	8	49 $\pm$ 1.9	25	2.5 $\pm$ 2.0	1 $\pm$ 1
109	22/12	April 29	18	44 $\pm$ 0.8	67	1.9 $\pm$ 0.7	9 $\pm$ 6
	28/18	April 1	12	48 $\pm$ 0.5	83	6.3 $\pm$ 1.5	68 $\pm$ 30
	30/20	April 1	8	47 $\pm$ 0.7	100	8.6 $\pm$ 2.6	99 $\pm$ 43
	25-40/20	April 29	11	46 $\pm$ 0.9	0	-	-
110	22/12	April 29	5	44 $\pm$ 1.2	40	1.2 $\pm$ 0.8	9 $\pm$ 5
	28/18	April 1	28	48 $\pm$ 0.6	93	7.6 $\pm$ 1.8	69 $\pm$ 18
	30/20	April 1	12	48 $\pm$ 1.1	100	10.1 $\pm$ 1.8	99 $\pm$ 26
	25-40/20	April 29	6	41 $\pm$ 2.5	17	0.7 $\pm$ 0.7	8 $\pm$ 8
111	22/12	April 29	23	45 $\pm$ 1.2	48	1.2 $\pm$ 0.4	15 $\pm$ 5
	28/18	April 1	28	52 $\pm$ 0.7	100	15.8 $\pm$ 2.2	126 $\pm$ 21
	30/20	April 1	15	50 $\pm$ 0.8	100	12.2 $\pm$ 2.0	135 $\pm$ 32
	25-40/20	April 29	14	52 $\pm$ 2.8	64	6.7 $\pm$ 2.2	99 $\pm$ 57
Atlantic	25-40/20	April 29	18	53 $\pm$ 2.3	83	5.3 $\pm$ 1.2	100 $\pm$ 42
	25-28/15-18	April 1	9	59	100	6.9 $\pm$ 0.6	213 $\pm$ 32
Blanka	25-28/15-18	April 29	4	62 $\pm$ 4.3	0	-	-
Deelree	25-28/15-18	April 29	5	49 $\pm$ 5.4	100	4.7 $\pm$ 1.1	50 $\pm$ 29
Spunta	25-28/15-18	April 29	4	56 $\pm$ 6.0	50	2.0 $\pm$ 1.2	14 $\pm$ 12
Cara	25-28/15-18	April 29	5	47 $\pm$ 0.9	60	5.7 $\pm$ 3.1	5.2 $\pm$ 2.5
Alpha	25-28/15-18	April 29	5	53 $\pm$ 2.5	60	3.1 $\pm$ 2.2	3.5 $\pm$ 2.0
	25-28/15-18	April 29	6	40 $\pm$ 1.7	33	0.8 $\pm$ 0.5	0.5 $\pm$ 0.3

(1) Harvest of most of the plants took place when 2-3 flowers were visible (38 to 57 days after planting); the few remaining plants were harvested 66 and 74 days after planting.

(2) Number of tubers (replicates) planted.

Table 12. The content of glycoalkaloids (mg/100 g fresh tuber weight $\pm$ standard error) of clones grown in the field during summertime in Israel (April 17 to July 17-26, 1994; Bet Dagan). Most tubers were ca. 20 mm in diameter.

Selection*			
temperature	Family	Clone	glycoalkaloids
Day 22°C	102	342	47.6 $\pm$ 0.7
Night 12°C	102	355	48.1 $\pm$ 2.5
	104	391	32.6 $\pm$ 0.6
	104	396	31.6 $\pm$ 2.1
	104	405	14.4 $\pm$ 1.0
	104	409	21.2 $\pm$ 0.6
	104	414	14.4 $\pm$ 0.2
	105	418	15.7 $\pm$ 2.2
	111	579	11.5 $\pm$ 0.4
Day 28°C	102	933	18.1 $\pm$ 0.9
Night 18°C	103	945	39.1 $\pm$ 0.3
	103	956	34.5 $\pm$ 0.5
	104	979	7.6 $\pm$ 0.3
	104	989	6.9 $\pm$ 0.5
	104	993	20.6 $\pm$ 2.2
	104	1000	17.4 $\pm$ 1.4
Day 30°C	104	91	27.6 $\pm$ 0.9
Night 20°C	104	100	21.0 $\pm$ 0.7
	104	101	14.0 $\pm$ 0.4
	105	121	27.4 $\pm$ 0.6
	107	199	19.4 $\pm$ 0.8
Day 25-40°C	104	670	19.1 $\pm$ 1.0
Night 20°C	104	675	19.3 $\pm$ 0.5
	110	808	28.4 $\pm$ 0.3
	110	809	19.8 $\pm$ 0.4
	110	823	38.6 $\pm$ 0.5

* Temperatures at the greenhouse where the clones were originally selected from TPS.

Table 13. Number of days to shoot emergence and flowering in different genomes of complex 4x-2x potato hybrids and check cultivar Atlantic under naturally occurring heat stress conditions in the field in Virginia.

Genomic composition	Number of days to shoot emergence	Number of days to flower
TAPB	37a*	70a
TAPC	39a	65a
TAPM	36a	68a
Atlantic	24b	60b

* Mean separation within columns by Student-Newman-Keul's test, 5% level.

Table 14. Yield parameters of different genomic compositions of complex 4x-2x potato hybrids and check cultivar Atlantic under naturally occurring heat stress conditions in the field in Virginia.

Genomic composition	Total tuber yield (g)	Number of tubers	Average tuber weight (g)
TAPB	790b*	13a	64b
TAPC	846ab	13a	72b
TAPM	857ab	13a	75b
Atlantic	972a	7b	138a

* Mean separation within columns by Student-Newman-Keul's test, 5% level.

Table 15. Frequency of tubers with the internal defects hollow heart, heat necrosis and second growth in 4x-2x potato hybrids of three genomic compositions compared to cv.

Atlantic under naturally occurring heat stress conditions in the field in Virginia.

Genomic composition	Frequency of		
	hollow heart	heat necrosis	second growth
TAPB	3.0b*	9.2b	5.7b
TAPC	8.3a	14.2b	8.2a
TAPM	3.7b	12.5b	8.5a
Atlantic	10.0a	37.7a	0.0c

* Mean separation within columns by Student-Newman-Keul's test, 5% level.

Description of cooperation

Cooperation between investigators in Israel and the US has been fine. Germplasm exchange in both directions, transmission of data sets electronically, visits, fax transmissions, and common attendance at a professional meeting have all facilitated communication.

Evaluation of research achievement

The goals of the proposal have largely been met. We have demonstrated that construction of potato hybrids through introgression of wild species with traits of interest, such as heat tolerance, will result in a population of potatoes with yield characteristics of potato cultivars but increased tolerance to stress. Surprisingly, it did not matter whether or not the diploid parents of 4x-2x hybrids were heat tolerant themselves in order to generate heat tolerant progenies. Gametic selection holds some promise if stress is applied either during anther culture or to pollen samples. However, the findings were only preliminary in this regard.

Conclusion

The complex hybrids exhibited several forms of heat tolerance both in Israel and in Virginia. They were able to tuberize under severe heat stress conditions in the field and they exhibited considerably less heat-induced internal defects while maintaining yield comparable to or better than the cultivar parent. However, they also expressed some undesirable traits (second growth, more and smaller tubers) associated with the unadapted parents. There was considerable variation

for all traits within these families, allowing selection of more adapted clones with greater heat tolerance than the cultivar parent.

Some of the selected heat tolerant complex hybrids, now in preliminary field tests, seem to have a combination of genes that facilitates superior performance in the field. The combination of genetic and physiological studies, i.e., the creation of new genomic combinations using unadapted germplasm with heat tolerance followed by screening and selection based on physiological knowledge, lead to the development of new heat tolerant potatoes. These selections represent a base from which new cultivars adapted to warm climates will eventually evolve. The diversity of potato germplasm with traits of economic interest may hold the key to adaptation of potato to nontraditional environments.

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