Theor Appl Genet (1991) 82:130–136

THEORETICAL
AND
APPLIED GENETICS

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

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Received August 3, 1990; Accepted September 26, 1990
Communicated by A. R. Hallauer

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 × Desiree and of Blanka × 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 × Desiree, and ca. 16% in progeny of Blanka × 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 conal year. The results of this study indicate that: (a) tolerance to heat is associated with earliness; however, differences in the response to heat exist 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, semiarid, and arid regions, the need arose to breed 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, as well as procedure 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 temperatures and minimum night temperatures are given in Table 2. Day length increased from 13 h on April 16 to 14 h 10 min on June 6. Twenty-five tubers of each cultivar were planted in a ridged row (one row per cultivar) in sandy soil, which was previously fumigated with methyl bromide to reduce soil diseases and seed growth and to provide uniform soil conditions. 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 compared to late-maturing genotypes, which form tubers and accomplish yield accumulation later and are exposed to 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 hot versus 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.

Heat tolerance in the glasshouse was evaluated 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 fifteen 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 ot 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 that varied in tuberization under high temperatures and that 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 cultivars Desiree, Cara, and Blanka was collected from plants grown in the open, and crosses between the three cultivars were produced in a glasshouse or in net houses. Due to insufficient seed set of Blanka (OP) and of the crosses Cara × Blanka and Desiree × Cara, these were not included in the progeny tests. The seeds were sown in speedling trays (Speedling Inc., Sun City/FL, USA) containing peat and vermiculite (2:1 v/v). The number of seedlings 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-cm^2 plastic pots in the cool glasshouse for further development.

After 88 days in the hot glasshouse, 50 of the seedlings that did not initiate tubers were transferred from each family 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 6). 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 of approximately 5 mm, 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

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
	Constante	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	Daily mean temperatures (°C)				Relative humidity (%)	
	Maximum		Minimum			
	1982	1983	1982	1983	1982	1983
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 °C 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 × D = Cara × Desiree; B × C = Blanka × Cara

Cool temperature, short day

D = 185
C = 185
C × D = 177

Cool temperature, long day

D = 173
C = 180
C × D = 178

Hot temperature, short day

D = 276
C = 275
C × D = 284
B × C = 295

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

D = 50
C = 50
C × D = 50
B × C = 50

planted in 10-cm^2 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 day length 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

Field trials. In two field trials conducted during late spring and summer, the plants of 14 potato cultivars were exposed to increasing temperatures and day length. 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 tu-

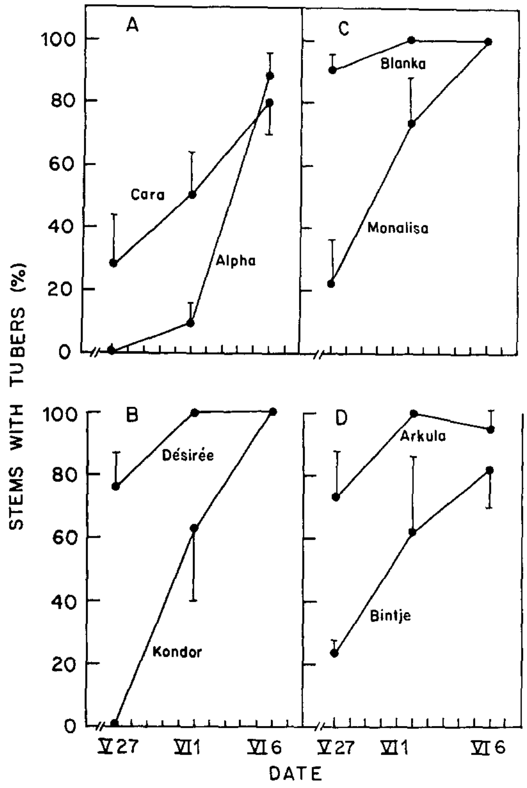

Fig. 1 A–D. Tuber formation percentage of stems with tubers in potato cultivars of various maturity classes grown in the field in Bet Dagan under relatively high temperature during the early summer season (1983). **A** later, **B** intermediate, **C** early, and **D** very early-maturing cultivars. *Bars*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

Table 4. The relative tuber yields (yield of each of the cultivars/the mean of all 14 cultivars × 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

Maturity class	Cultivar	Relative tuber yield		
		1982	1983	Mean
Very early	Arcula	204	105	155
	Bintje	83	1	42
	Cleopatra	176	139	158
	Constante	79	17	48
Early	Gracia	7	79	43
	Blanka	249	310	280
	Monalisa	80	101	91
	Murillo	71	–	–
Intermediate	Kennebec	76	140	108
	Diamant	164	231	198
	Desiree	78	148	113
	Kondor	89	13	48
Late	Cara	0	13	7
	Alpha	41	9	25

Table 5. The effect of temperature on tuberization 20 and 42 days after exposure to conditions in the cool (cool) versus 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
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
Desiree	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	1.8±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

ber initials on May 27; however, more than 60% of the stems of Kondor, but 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 (Table 4). Blanka followed by Diamant, Cleopatra, and Arcula had high relative tuber yields, whereas the late-maturing cultivars, Cara and Alpha, had low tuber yields (Table 4). Accordingly, severe yield losses have been recorded in Cara and Alpha when grown in the hot summer, compared to 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) versus 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.

Glasshouse experiments. The rate of tuber formation under favorable temperature conditions in the cool glasshouse is given in Table 5. 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 glasshouse – 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

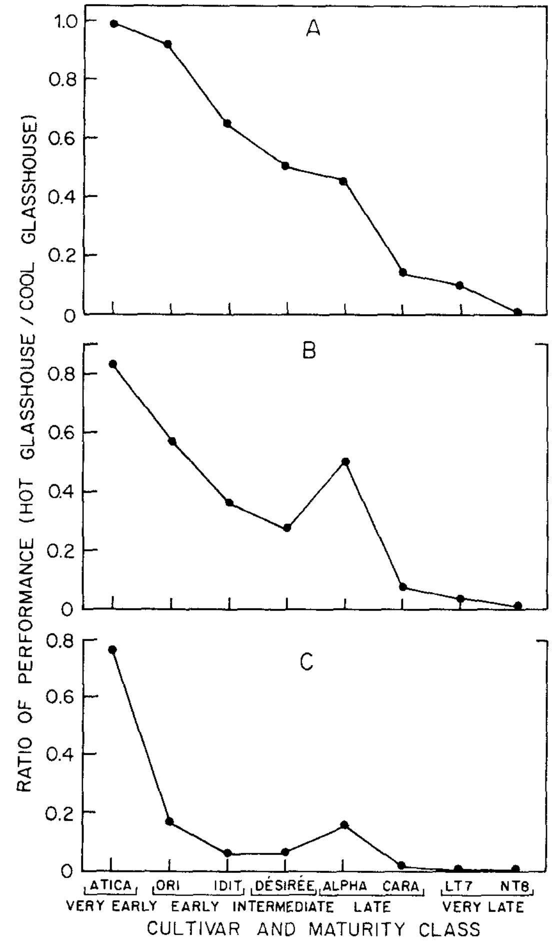

Fig. 2A–C. Tolerance to heat, estimated as the ratio of performance in the hot glasshouse to performance in the cool glasshouse, of: **A** number of stems with tuber initials or tubers; **B** number of tubers per stem; and **C** yield of tubers per stem

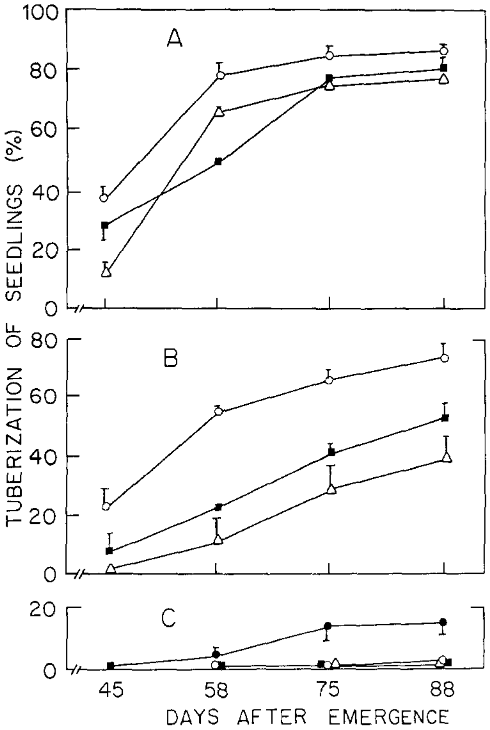

Fig. 3A–C. The effect of temperature and of day-length on tuberization of seedlings (percent of total population) grown from open-pollinated seeds of Desiree (o) and Cara (▵), and from hybrid seeds of Cara × Desiree (■) and Blanka × Cara (●). **A** Cool glasshouse, 13 h photoperiod; **B** cool glasshous, 16 h photoperiod; **C** hot glasshouse, 13 h photoperiod

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. 2); however, differential response to heat could be detected in cultivars of the same maturity class.

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 × Desiree, and Desiree, respectively (Fig. 3A). 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. 3B). However, in the progeny of the earlier tuberizing cultivar Desiree (which initiates tubers under longer photoperiod), the retardation of tuber initiation by the long days was less compared to 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 × Desiree was intermediate, but closer to that obtained for progeny of the maternal parent Cara than in progeny of the male parent Desiree (Fig. 3B).

High temperatures strongly inhibited tuber initiation (Fig. 3C). In the progeny of Desiree and Cara × 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 5). The behavior of the Cara × Desiree population is interesting: tuber initials were visible concomitantly in the Cara × 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 × Desiree progeny (1.72±1.02%) was similar to that of the progeny of Cara (1.42±0.97%), and both were lower than the tuberization rate of Desiree progeny (3.92±1.13%). This resembles the behavior of the Cara × Desiree progeny at favorable temperatures (Fig. 3A) and in long photoperiod (Fig. 3B). All three independent experiments (Fig. 3A–C) indicate that in a seedling population of a hybrid, the control of tuber initiation timing may be independent of the control of the rate of tuberization, and that each of these characters could be influenced by either parent. In the seedling population of Blanka × Cara, however, both timing and rate of tuber initiation differed greatly from the seedling population of Cara (Fig. 3C). 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 temperature timing and rate in their hybrid population (Blanka × Cara) from the seedling population of Cara (Fig. 3C).

Seedlings that 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 × Desiree, and Cara, respectively, formed tubers (Table 6). These values were close to those obtained with seedlings that were not exposed to high temperatures and examined 78 days after emergence (values in parentheses, Table 6), indicating that the inhibitory effect of high temperatures on tuber formation was 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. 4). Clones of Desiree progeny selected for tuber formation in the cool glasshouse under long days tuberized faster than those selected under short

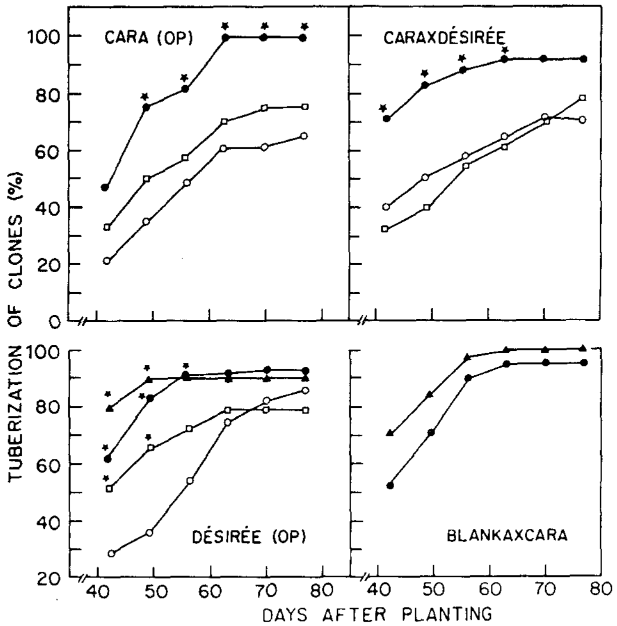

Fig. 4. Tuberization in 1st-year clones (percent of total population) grown form small tubers in a hot glasshouse with a 13 h photoperiod. The tubers were harvested from seedlings grown under various conditions: cool glasshouse, 13 h photoperiod (o); cool glasshouse, 16 h photoperiod (□); hot glasshouse 13 h photoperiod (▲); 69 days in the cool glasshouse after 88 days in the hot glasshouse (●), 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)

Table 6. 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 nontuberizing 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 × Désirée	50 (71)
Blanka × Cara	50 (–)

days at 40–50 days after planting in the hot glasshouse (Fig. 4), 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 × Desiree (Fig. 4).

Tubers of the first clonal generation, harvested from seedlings that were first exposed to high temperature but formed tubers after their transfer to the cool glasshouse, had higher tuberization rates in Cara, in Cara × Desiree and, to a lesser extent, also in Desiree, compared with the nonselected clones of the same families (Fig. 4). In Desiree and in Blanka × Cara, clones selected by preexposure to hot conditions followed by cool temperatures were similar in their tuberization behavior to those selected in hot glasshouses (Fig. 4).

Discussion

The differential response of potatoes to high temperatures and the association of early maturation with tolerance to heat has been clearly shown (Fig. 2). 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 favoring tuber formation (Table 5), 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 × Cara, where heat tolerance was greatly enhanced by the heat-tolerant parent Blanka, yielded sufficient selections under these conditions (Fig. 3C). 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 percentages of tuberizing seedlings came close to that of seedlings that were not exposed to heat and formed tubers in the cool glasshouse (Table 6). 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. 4). 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 vigorous haulm growth under heat stress, 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, is controlled genetically, and that heat-tolerant genotypes might be identified in the progeny of a heat-susceptible parent. It also illustrated that heat tolerance might be enhanced by crossing a heat-tolerant cultivar such as Blanka with a heat-susceptible cultivar such as Cara (Table 6), 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. 4).

Acknowledgements. The authors thank Prof. R. E. Veilleux (Department of Horticulture, VPI and SU, Blacksburg/VA, USA), Dr. G. C. C. Tai (Agriculture Canada, Frederiction), and Drs. S. Cohen, A. Levy, and M. Pilowsky for helpful comments on the manuscript. This work has been supported by Grants US-994-85 and US-1196-86 from the United States-Israel Binational Agricultural Research and Development Fund (BARD). Contribution of the Agricultural Research Organization, The Volcani Center, Bet Dagan, Israel, No. 2820-E 1989 series.

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