HEAT TOLERANCE IN TUBER BEARING *SOLANUM* SPECIES: A PROTOCOL FOR SCREENING[1]

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Abstract

Three hundred nineteen accessions of 59 tuber bearing species of *Solanum* were screened for heat tolerance. The ability to produce shoot growth at high temperature (30 to 40 C) was tested initially. Since shoot growth is affected by tuberization, plants were grown at 18-h photoperiods to minimize tuber induction in all accessions. Fifty-one accessions of seven species were screened in three separate years to assess the stability of the estimates of heat tolerance. Shoot fresh weights at the high temperature were significantly correlated (r=0.7) from year to year, as were ratings for plant vigor at the high temperature (r=0.5).

Accessions that showed good shoot growth at the high temperature were screened again for tuberization under short days and high temperature (30 to 40 C). In general, tuberization was highly variable, but a few species and a few accessions showed consistent tuberization at 30 to 40 C.

Compendio

Se tamizaron 319 entradas de especies de *Solanum* formadoras de tubérculo, para tolerancià al calor. Inicialmente se probó la habilidad de generar el desarrollo de brotes a altas temperaturas. Desde que el desarrollo de brotes es afectado por la tuberización, las plantas se dejaron crecer a fotoperiodos de 18 horas para minimizar la inducción de formación de tubérculos en todas las entradas. Se tamizaron 51 entradas de siete especies, en tres años separados, para evaluar la estabilidad de los estimados de tolerancia al calor. Hubo una correlación significativa (r=0.7) de año a año en el peso fresco de los brotes a temperatura alta, así como también en los valores para vigor de la planta a temperatura alta (r=0.5).

Las entradas que mostraron un buen desarrollo a temperatura alta se tamizaron nuevamente para tuberización bajo condiciones de día corto y temperatura alta (30-40 C). En general, la tuberización fué altamente variable, pero unas pocas especies y unas pocas entradas mostraron tuberización consistente entre 30 y 40 C.

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Introduction

Introduction of genetic traits from wild relatives of a cultivated species can improve adaptation to a specific crop environment. More than twenty wild *Solanum* species have already been introduced into some forty-nine potato breeding programs currently in progress in North America (15). Useful traits include resistance to a range of pests and, to some extent, environmental stresses. There is interest in breeding potato cultivars adapted to the lowland tropics (19), where night temperatures above 20 C and day temperatures as high as 40 C impair yield in non-adapted cultivars (4, 5, 8). *S. tuberosum* has a relatively narrow genetic base (18); and since high temperature stress affects a number of physiological processes (9, 14), it is expedient to look for heat tolerant traits among the many wild, tuber bearing species in the genus.

Our primary objective was to examine accessions from the collection of the Inter-Regional Potato Introduction Project (11) for the presence of traits that might be useful in breeding for heat tolerance. In this connection we screened in the greenhouse 319 accessions of 59 *Solanum* species during 1985 and 1986. Because complex genetic characteristics like heat tolerance frequently show gene x year interactions, some indication of the stability of the parameters used to assess heat tolerance from year to year was required. To assess stability, 51 accessions of seven species were screened for three consecutive years.

Two aspects of heat tolerance were evaluated in the screening: 1) the ability of plants to produce shoot growth under high temperatures and long photoperiods, and 2) their ability subsequently to produce tubers under high temperatures and short photoperiods.

Materials and Methods

Growing Conditions

The two plastic greenhouses used in these experiments were operated as described previously (1). The "hot" greenhouse was heated to approximately 30 C at night and was allowed to reach approximately 40 C during the early afternoon before ventilation was started. The mean hourly temperature in the hot house varied between 35 C and 42 C during the day, depending on the intensity of the sunlight. On cloudy days a gas furnace was activated for supplementary heat. The "ventilated" greenhouse served as the control treatment. It had open sides (covered with polyester drapery batiste to keep out insects), and a large fan provided further ventilation so that maximum temperatures typically varied between 30 C and 40 C during the day and minimum temperatures varied between 15 C and 25 C at night. During hot weather the maximum daily temperatures were similar between the two greenhouses; but the ventilated house was cooler in the mornings and late afternoons, and especially at night. Previous experience had shown that although temperatures in the ventilated house on sunny days were considerably higher than outside, potato growth and tuber production were comparable to what was obtained under field conditions (1). Natural daylength, which decreased from 15 h to 13 h during the season, was lengthened in both houses to 18 h with 100-watt incandescent lamps at an intensity of 1 μE m^{-2} s^{-1}.

Seedlings were grown from true potato seed in the ventilated house and were transplanted 3 to 4 weeks after sowing into 10-cm plastic pots containing Cornell Mix A (3). After 1 to 2 weeks, during which the plants became established, 27 plants of each accession were put into each plastic greenhouse.

Temperatures in the ventilated house were fairly uniform throughout the house at any given time. Because of the greater temperature variability from location to location in the hot house, the 27 plants in an accession were divided into three blocks of nine plants per replication. The replications were distributed in the hot greenhouse according to three blocking factors: a) the north-south gradient, across the width of the house; 2) the east-west gradient, along its length; and 3) the position on the bench of a row of nine plants. Rows were allocated randomly within a block. Border plants were grown on the outside edges of each bench.

Plants were grown for 25 to 30 days under these conditons with an 18-h photoperiod, were fertilized weekly with a 15-7-14 N-P-K solution, and were watered automatically.

Assessment of Shoot Growth

After the 4-week treatment period each of the 3 replications in the hot house was visually assessed for vigor on a scale of 1 to 9 by two separate observers. Vigor ratings were based upon leaf color, necrosis, chlorosis, leaf rolling, leaf angle, plant size, and leaf size. The plants in these three replications and the nine plants of each accession from the ventilated house were then cut at the soil line, and the shoots in each replication were weighed together. In some cases the dry weights were also determined: although this would be a more satisfactory variable for making comparisons, the dry weight data were incomplete.

Selections for heat tolerance with respect to shoot growth were then made, based upon mean vigor ratings and shoot weights.

Assessment of Ability to Tuberize in the Heat

Of the accessions identified as relatively heat tolerant, the plants remaining in the ventilated house were transplanted to 15-cm clay pots containing Cornell Mix A, and nine plants of each were grown for 2 weeks under short photoperiods in each house to encourage induction to tuberize. Short daylengths were provided by drawing dark shade cloth over the plants from 1700 hours until 0800 hours. After the exposure to short photoperiods, plants were assessed for levels of induction to tuberize in the leaves by rating the tuberization of leaf-bud cuttings (7). Single leaf-bud cuttings were taken from young shoots and placed in the mist bench under constant illumination for 14 days, with axillary buds buried in Cornell Mix A. Bud development was rated on a scale of 1 to 5, where 1 represents a sessile tuber, indicating the highest degree of induction. A rating of 5 indicates no bud development, the lowest level of induction, and intermediate values represent intermediate levels of induction (7). Plants from which cuttings had been removed were left in their respective greenhouses for 4 to 5 weeks under natural daylength until tuber harvest.

Results

Shoot Growth

A brief summary of the data from accessions that underwent only one screening is presented in this paper: a complete report is available on request from the authors. Table 1 shows the species in which more than half of the accessions were deemed heat tolerant as judged by the following criteria: an average vigor rating in the hot house >6, and either a fresh weight ratio (hot:ventilated) >0.6 or an average fresh weight in the hot house greater than the mean for all accessions grown in the hot house.

For accessions screened in three separate years, the parameters used to assess heat tolerance were hot house vigor ratings, fresh weight in the hot house, and ratio of fresh weights between hot and ventilated houses (Table 2).

TABLE 1. — Solanum *species that showed heat tolerance in more than half of the accessions tested based on shoot growth at 30 C to 40 C.*

Species	Number of accessions screened	Vigor rating, hot house[1,2]	Fresh weight, hot house g/9 plants[1]	Fresh Weight ratio (hot:ventilated)[1]
S. berthaultii	9	6.8	108	0.67
S. bulbocastanum	12	6.3	100	0.64
S. chacoense	16	6.3	203	0.76
S. commersonii	6	6.5	147	0.68
S. demissum	11	6.5	139	0.64
S. fendlerii	9	5.9	140	0.60
S. kurtzianum	12	6.3	197	0.80
S. microdontum	6	6.4	261	0.37
S. vernei	5	6.3	106	0.71

[1]Based on means for all accessions within each species. (Note that although more than half of the accessions of *S. fendlerii* had mean vigor ratings >6.0, the mean rating for all accessions was 5.9.)

[2]Ratings were on a scale of 1 to 9 where 9=absence of symptoms of heat stress, 1=complete necrosis, and 8 through 2 indicated increasing severity of heat stress symptoms.

TABLE 2. — *Summary of growth parameters measure in 51 accessions during three cycles of heat screening at 30 C to 40 C*[1].

Species	Accession number	Vigor rating, hot house[2]	Fresh weight of shoots (g/9 plants) Ventilated house	Hot house	Fresh weight ratio of shoots (Hot:Ventilated)
S. brachycarpum	PI 255514	6	75	36	0.67
	PI 275179	6	178	61	0.34
S. bulbocastanum	PI 243504	5	167	106	0.65
	PI 243513	5	162	96	0.72
	PI 275184	6	166	90	0.54
	PI 275187	6	181	113	0.64
	PI 275195	5	146	92	0.54
	PI 347757	6	213	157	0.76
	PI 347758	7	115	93	0.87
	WRF 1565	6	120	105	0.69
S. chacoense	PI 175401	5	464	264	0.58
	PI 197760	7	393	282	0.72
	PI 209411	7	253	219	0.99
	PI 275141	6	250	84	0.42
	PI 320285	8	270	168	0.64
	PI 320290	7	341	306	0.95
	PI 414143	6	360	256	0.77
	PI 458309	5	323	156	0.54
	PI 473402	6	306	243	0.80
S. demissum	PI 160230	5	149	46	0.44
	PI 161149	6	211	96	0.61
	PI 161151	6	231	92	0.51
	PI 161365	6	161	86	0.54
	PI 161693	6	198	103	0.53
	PI 175411	6	235	148	0.67
	PI 186551	6	187	93	0.54
	PI 230559	6	209	125	0.56
	PI 275206	7	374	187	0.55
	PI 338618	7	304	204	0.68
	PI 347760	6	194	53	0.37
S. phureja	PI 275110	4	245	85	0.42
	PI 283121	4	149	45	0.33
	PI 320349	5	143	80	0.68
	PI 320349	5	256	126	0.47
	PI 320372	4	225	106	0.42
	PI 195198	3	191	72	0.37
	PI 225665	5	181	115	0.79
	PI 225674	5	247	97	0.42
	PI 243463	4	228	76	0.33
S. stoloniferum	PI 160224	4	228	44	0.35

[1]Values represent means from three separate years. Therefore the ratios in the last column are not exact quotients of the values in the two preceding columns.

[2]Ratings were on a scale of 1 to 9 where 9=absence of symptoms of heat stress, 1=complete necrosis, and 8 through 2 indicated increasing severity of heat stress symptoms.

TABLE 2. — *Continued.*

Species	Accession number	Vigor rating, hot house[2]	Fresh weight of shoots (g/9 plants) Ventilated house	Hot house	Fresh weight ratio of shoots (Hot:Ventilated)
	PI 161171	5	270	89	0.37
	PI 195167	5	299	126	0.43
	PI 205510	7	186	88	0.46
	PI 239411	5	216	136	0.54
	PI 255532	7	185	107	0.61
	PI 275247	6	220	148	0.51
	PI 283109	7	104	64	0.67
S. vernei	PI 320333	5	301	74	0.30
	PI 458372	6	256	74	0.53
	PI 458374	5	215	41	0.27
	PI 473304	6	282	110	0.64

[2]Ratings were on a scale of 1 to 9 where 9=absence of symptoms of heat stress, 1=complete necrosis, and 8 through 2 indicated increasing severity of heat stress symptoms.

The seven species that were included all three years were chosen for their heat tolerance or for the range of heat tolerance that their respective accessions had displayed in initial screenings. The vigor ratings for the individual accessions in the hot house correlated reasonably well from year to year, as did fresh weights in the hot house; but the ratio of fresh weights (hot:ventilated) correlated significantly only in the comparison between 1985 and 1987 (Table 3).

Tuberization Under Heat Stress

Levels of induction to tuberize in leaves, as measured by tuberization on cuttings taken from plants exposed to short photoperiods, were highly variable in both the hot and the ventilated houses. The species listed in Table 4 showed relatively high induction to tuberize on leaf-bud cuttings, based upon a single time of screening. More than half the accessions tested from these species were superior to the overall mean levels of induction from all accessions tested at the respective times. The mean induction rating over all accessions after short day treatment in the hot house was 3.6 on the 1 to 5 scale. For plants under short days in the ventilated house it was 2.8. The higher ratings in the hot house indicated less induction to tuberize.

Tuber yield was extremely variable in both hot and ventilated houses. Some plants grew only a mass of stolons; whereas others, sometimes even within the same accession, yielded as much as 100 g per plant in fresh weight. Table 4 indicates the number of accessions that produced tubers in the hot house in the species deemed heat tolerant with respect to induction

TABLE 3. — *Pearson correlation coefficients for dependent variables used to assess heat tolerance in ventilated and hot (30 C to 40 C) greenhouses.*[1]

Years correlated	Vigor rating, hot house[2]	Fresh weight of shoots: Hot house	Fresh weight of shoots: Ventilated house	Fresh weight ratio of shoots (Hot:Ventilated)
1985 v 1986	0.48 ***	0.74 ***	0.27 ns	0.27 ns
1986 v 1987	0.50 ***	0.68 ***	0.31 *	0.10 ns
1985 v 1987	0.52 ***	0.76 ***	0.51 ***	0.28 *

[1]P≤0.001, P≤0.05, and not significant are denoted by ***, *, and ns, respectively.
[2]Ratings were on a scale of 1 to 9 where 9=absence of symptoms of heat stress, 1=complete necrosis, and 8 through 2 indicated increasing severity of heat stess symptoms.

TABLE 4. — Solanum *species that were relatively heat tolerant at 30 C to 40 C with respect to levels of induction to tuberize in the leaves.*

Species	Number of accessions screened	Mean induction rating[1]	Number of accessions tuberizing in hot house
S. berthaultii	9	2.9	2
S. chacoense	10	3.5	6
S. demissum	8	2.9	5
S. jamesii	2	3.1	2
S. kurtzianum	6	3.1	5
S. papita	5	2.7	1
S. spegazzinii	2	3.4	1
S. stoloniferum	4	2.4	3
S. sucrense	2	2.7	1

[1]Induction ratings indicate degree to which leaf-bud cuttings tuberized, on a 1 to 5 scale, where 1=strongest induction.

ratings. A few of the accessions that were screened for tuberization two or three times yielded tubers in the hot house each time they were grown (Table 5).

In Vitro *Culture*

Heat tolerant and heat sensitive accessions within a number of species were cultured *in vitro* to provide material for future investigations on heat tolerance. They have been tested by nucleic acid hybridization for freedom from Potato Spindle Tuber Viroid and for freedom from viruses by ELISA, and are available on request.

TABLE 5. — Solanum *accessions that consistently yielded tubers in the hot greenhouse (30 C to 40 C) after a short day treatment.*

Species	Accession	Number of years screened
S. bulbocastanum	PI 275184	2
	PI 347757	2
S. chacoense	PI 197760	3
	PI 320285	3
S. demissum	PI 161365	2
	PI 161693	2
	PI 175411	2
	PI 186551	2
	PI 230559	3
	PI 275206	3
S. stoloniferum	PI 255532	2
	PI 275247	2
	PI 283109	2

Discussion

In potato, heat tolerance requires the ability to produce adequate shoot growth under heat stress, and then to partition assimilates to tubers. Presumably the genetic traits associated with the ability to carry out shoot growth under heat stress are distinct from those associated with tuber initiation and growth. We therefore screened separately for these traits.

To assess heat tolerance with respect to shoot growth, it was desirable to carry out the screening under photoperiods that eliminated tuberization. At all temperatures, shoot growth is strongly affected by the degree to which the plants have become induced to tuberize (2). In a highly induced plant most of the assimilates are diverted to tuber growth at the expense of canopy development. Screening at a potentially inductive photoperiod would complicate the assessment of heat tolerance of shoot growth: the factor of high temperature, which generally discourages induction to tuberize (10, 13), would be confounded with the innate sensitivity of the genotype to photoperiod (6). It would therefore be difficult to distinguish whether poor shoot growth in a given accession was attributable to high temperature stress (indicating sensitivity to heat) or merely to the tendency to become highly induced to tuberize early in development before a good canopy had been established (thus reflecting the ability to form tubers even under high temperatures—an aspect of heat tolerance). Our solution to the problem was to screen for shoot growth under 18-h photoperiods and then make a second screening under short photoperiods for tuberization.

Two estimates of heat tolerance for shoot growth were reasonably consistent from year to year: vigor rating in the hot house and fresh weight in the hot house. The ratios of fresh weights (hot:ventilated) were not as well correlated between years, probably because temperatures from one year to the next in the ventilated house were more variable than in the hot house. (The environments in both houses varied with outside conditions, but the range was more restricted in the hot house.) The generally lower correlations from fresh weights of shoots in the ventilated house over years (Table 3), compared to those from the hot house, tend to support this conclusion. Furthermore, the one year-to-year comparison where the ratios are significantly correlated, 1985 vs. 1987, also shows the only highly significant correlation between fresh weights of shoots in the ventilated house (Table 3). Another factor probably contributing to the variability in the ventilated house was the smaller number of plants grown per accession.

Results from the ventilated house were intended to show whether the good performance of a given accession in the hot house was associated with "true" heat tolerance or only with overall genetic potential for prolific growth. Examination of growth ratios between the two houses should help answer this question. An accession with a high fresh weight in the hot house and a high ratio of hot to ventilated fresh weights would be considered relatively insensitive to heat stress, whereas a high fresh weight but a low fresh weight ratio would indicate an accession with overall growth potential that compensated for its sensitivity to heat stress. Although the year-to-year variability in fresh weight ratios between the two houses casts doubt upon the reliability of the comparisons, some of the accessions produced high shoot weights in both houses, suggesting that their apparent heat tolerance was associated with overall growth potential. Better temperature control in the ventilated house could be expected to reduce the variability among years.

The maintenance of a photosynthetically active leaf canopy is a prerequisite to good tuber yield (20, 21), and there is evidence of a correlation between rate of photosynthesis and heat tolerance in several wild potato species (17). For this reason, and also because the screening for shoot growth is more easily accomplished, only accessions that demonstrated reasonable shoot growth at high temperatures were screened for tuberization.

The two estimates of heat tolerance for tuberization, induction of leaves to tuberize in the hot house and tuber yield in the hot house, were not always correlated. The ten accessions of *S. chacoense* had the lowest mean induction rating of any of the species, but six out of ten of these accessions subsequently yielded tubers in the hot house. In contrast, accessions of *S. berthaultii* showed one of the highest mean induction ratings, yet only two out of nine accessions produced tubers in the hot house (Table 4). Induction ratings are not necessarily a reliable indicator of final tuber yield, canopy size being another important factor (12). Furthermore, tuberization can be inhibited by high (30 C) soil temperature, irrespective of the level of induction in the leaves (16).

The major objective in these experiments was to screen for the ability of accessions to make good shoot growth under prolonged exposure to high day and night temperatures: differences in this trait showed up very well. The screening procedures were not designed to test for plant emergence from hot soil, response to acute heat stress, the indirect effects of high temperature such as drought and subsequent nutrient stress, or adverse effects of heat stress on tuber quality. Data for tuberization were generally more variable than for shoot growth, but a few species and a small number of accessions indicated potential not only for good shoot growth under high temperature stress, but also for consistent tuber production. Since all plants were grown from seed, genetic variation among plants of the same accession can be expected.

Many of the species that showed good levels of heat tolerance are already present in the pedigrees of potato varieties released between 1956 and 1985 in North America (15). *S. chacoense* is found in 18 varieties, *S. acaule* in 17, and *S. demissum* is in the pedigree of 74 North American varieties. A list of six accessions (Table 6) that consistently demonstrated exceptional heat tolerance with respect to both shoot growth and tuberization is presented, based on the data in Tables 2 and 5. Some of them are available *in vitro* from the authors, or they may be obtained as seeds from the Inter-Regional Potato Introduction Station at Sturgeon Bay, Wisconsin.

TABLE 6. — *Accessions that showed consistently outstanding heat tolerance at 30 C to 40 C in terms of shoot and tuber growth.*

Species	Accession number
S. bulbocastanum	PI 347757
S. chacoense	PI 197760
	PI 320285
S. demissum	PI 175411
	PI 275206
S. stoloniferum	PI 255532

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