BARD

FINAL REPORT

PROJECT No. US-427-82

The Physiology of Heat Tolerance in Potato — A Simulation Modeling Approach

E.E. Ewing, M. Dinar, J. Rudich (Deceased), G.W. Fick

1987

June 25, 1987

BARD
P.O.B. 6
Bet Dagan, 50250 ISRAEL

BARD Research Project No. US-427-82

Title of Research Project:
The physiology of heat tolerance in potato--a simulation modeling approach

Name and address of Investigators:

Principal Investigator: Elmer E. Ewing (Cornell University)
Cooperating Investigators: Menachem Dinar (Israel), Jehoshua
Rudich [deceased] (Israel), Gary W.
Fick (Cornell)

Name and Address of Affiliated Institutions:

Principle Institution: Cornell University, Ithaca, N.Y.
14853
Cooperating Institution: Hebrew University, Faculty of
Agric., P.O. Box 12, Rehovot,
Israel

Project's Commencement date: October 1, 1983

Type of report: 1st Annual ☐ 2nd Annual ☐ Final ☒

Signatures:

Principle Investigator

EE Ewing

Institution's Authorized Official
(signature and official stamp)

[Signature]

M. Ottolenghi
PROFESSOR MICHAEL OTTOLENGHI
VICE PRESIDENT for RESEARCH
and DEVELOPMENT

This report is dedicated
to the memory
of Professor Jehoshua Rudich,
whose penetrating mind,
intellectual integrity,
and kind regard for others
inspired all who were privileged
to know him.

TABLE OF CONTENTS

I. ABSTRACT.....	1
II. OBJECTIVES.....	2
III. BODY OF THE REPORT.....	2
A. Growth Analysis.....	3
1. Field experiments.....	3
2. Greenhouse experiments.....	16
B. Time and Method of Heat Stress.....	24
1. Stage of growth at heat stress.....	24
2. Effect of night temperature on final organ dry weight...	37
3. Day temperature X daylength.....	37
4. Cultivar X daylength X temperature.....	37
5. Soil temperature.....	44
C. Possible Associations between Growth and Maintenance Respiration and Heat Tolerance.....	52
D. Heat Tolerance and Photosynthesis.....	65
1. Experiments with <u>S. tuberosum</u>	65
2. Maximal rates of O ₂ evolution in wild <u>Solanum</u> species..	87
3. Fluorescence.....	90
E. Effects of Heat Stress on Developmental Patterns and Partitioning.....	94
1. The effect of temperature and photoperiod on tuberization of potato cuttings.....	94
2. Rate of leaf production and decline of relative growth rate.....	98
3. Effects of heat stress on carbon translocation and partitioning of assimilates throughout the season.....	107
4. The effects of day and night temperatures on carbon uptake, translocation, and its partitioning in three cultivars.....	108
5. Carbohydrate analysis and sucrose hydrolysis.....	120
6. Effect of photoperiod and temperature on leaf starch accumulation.....	121
F. Simulation Models.....	128
G. Overall Summary and Conclusions.....	141
H. Acknowledgements.....	150
I. Literature Cited.....	150

IV. DESCRIPTION OF COOPERATION.....	154
V. EVALUATION OF THE RESEARCH ACHIEVEMENTS.....	155
VI. LIST OF PUBLICATIONS.....	157

I. ABSTRACT

Ordinary potato (Solanum tuberosum L.) cultivars grown in hot locations give low tuber yields. Heat tolerant types had been identified, but little was known about the bases for their tolerance. Objectives were to identify the differences among potato cultivars in their reactions to heat stress; to investigate the factors controlling growth and development; and to incorporate such information into an explanatory model.

A common set of potato cultivars from diverse genetic backgrounds was studied in Israel and New York for their reactions to high temperatures. Differences were detected among the cultivars in their responses to heat stress with respect to both respiration and photosynthesis, but the clearest differences were in the partitioning of assimilate. Sensitive cultivars responded to heat by increased partitioning of ^{14}C to shoots at the expense of tubers. High air temperatures apparently reduced the ability of leaves to produce the stimulus for tuberization, whereas high soil temperatures prevented the expression of the induced condition. Tolerant cultivars such as 'Norchip' became induced to tuberize even at high air temperatures. Heat stress was most harmful to tuberization under long photoperiods.

After $^{14}\text{CO}_2$ labeling of leaves, an increase in the level of the labeled sucrose and a decrease in the starch fraction were observed in response to heat stress in tubers of the heat sensitive cultivar. Heat stress caused a marked decrease in sucrose synthetase activity of tubers, especially in the heat sensitive cultivar; but shoots of the sensitive cultivar showed increased sucrose hydrolysis. Heat stress depressed leaf starch synthesis.

The physiological model "POTATO" was improved and tuned. The less complex model from Israel has also been tuned for New York.

II. OBJECTIVES

The original objectives listed in the research proposal were to:

- a) Carry out growth analyses on potato cultivars grown in Israel and New York, comparing the same set of heat sensitive and tolerant clones at both locations.
- b) Investigate the physiological bases for differences revealed in the growth analyses, with emphasis on information that can be incorporated into a computer simulation model.
- c) To the extent possible within the time available, utilize the information obtained in pursuing the first two objectives to develop an explanatory model of growth and development in the potato.

We adhered to these three objectives throughout the project.

III. BODY OF THE REPORT

Potatoes are known to grow best in cool climates--hot growing conditions generally give severe reductions in tuber yields. Nevertheless, many reports indicate that it is possible to find within the species a substantial degree of genetic tolerance to heat. The purpose of this project was to investigate the physiology of heat tolerance.

It seemed likely that a number of different traits might contribute to such a broad phenomenon as heat tolerance, so we have included in our experiments a broad range of germ plasm. We have tried to use the same clones and cultivars at both locations so that our experimental results would be directly comparable. Although quarantine problems make it difficult to exchange genetic material, and the potential of disease spread complicates the rapid multiplication of genetic stocks, we have largely accomplished this goal of shared germ plasm through the use of in vitro transfer and multiplication.

The cultivars and clones used in common included 'Norchip', 'Katahdin', 'LT-1', 'C1-884', 'C14-343', and 'Desiree'. The first two are widely accepted commercial cultivars in the U.S., while the last is a popular cultivar in Europe, Israel, Southeast Asia, and North Africa. C1-884 and C14-343 are Neo-tuberosum clones derived from South American "Andigena" types via a recurrent selection breeding program at Cornell University. LT-1 is from the International Potato Center (CIP) potato breeding program and resulted from a cross between the late German cultivar 'Aguila' and Katahdin. The three clones and Desiree all have displayed some degree of heat tolerance in the field. Norchip, while not selected for heat tolerance, has exhibited heat tolerance in an artificially heated greenhouse at Cornell University (Ben Khedher and Ewing, 1985). Katahdin was included as a "standard" for comparison to the heat tolerant cultivars. Katahdin is broadly adapted to temperate areas but has not been reported to possess heat tolerance. In some experiments the European cultivars 'Up-to-Date' or

'Alpha' were used as heat sensitive standards instead of Katahdin. (For convenience we will hereafter refer to the numbered clones as cultivars, although they have not been released as such.)

The first step in our research was to carry out growth analyses of cultivars that reportedly possess heat tolerance. We wanted to confirm their tolerance and also to characterize their growth and development in hot and cool environments. Ten growth analyses were made or are underway on the same group of cultivars in the field. These cover a wide range of environments ranging from tropical lowlands and highlands to the temperate zone. Hourly meteorological data were also included. No growth analysis was made in the field in Israel under this project, but past research there has provided a great many data sets for the Desiree cultivar grown in the spring and fall seasons in the Negev. These will be available for model testing and validation along with the data sets from the other field locations. Additionally, similar experiments were carried out in greenhouses at both Rehovot and Cornell. The growth analysis experiments are described in Part A.

Part B describes the results of other experiments carried out in artificially controlled environments. Cultivars were compared for their response to heat stress applied at different times of the day, at different stages of growth, to different parts of the plant (above ground vs. underground), and in different combinations with photoperiod treatments.

Part C examines cultivar differences in dark respiration as affected by heat stress, and Part D deals with similar experiments on photosynthesis. The experiments in Part E are concerned with partitioning of assimilate to tubers and other organs.

Part F describes improvements to an explanatory simulation model that is being used to help understand how differences in physiological traits would contribute to heat tolerance. Tuning of a second model is also presented. The work in all of the previous parts is providing information for improving the models, which in turn should provide a better understanding of how differences among cultivars are related to heat tolerance.

A general summary and conclusions are in Part G, with a designation of the part that was summarized at the end of each paragraph.

A. Growth Analysis

1. Field experiments

Two growth analysis experiments were carried out at the Cornell University Vegetable Research Farm under this project. In addition similar experiments at a number of tropical locations have been partially supported under this project. We have linked our efforts to other research projects having similar objectives, so that the scope of the research could be enlarged. However, in all of these cooperative projects we have coordinated the planning so that the information obtained will be directly applicable to

the objectives of this project. For example, the same set of cultivars and clones has been included, and the data sets collected and procedures followed have been standardized. We have helped plan and coordinate all these experiments, some of which will continue into the future. Besides this, we have grown and shipped the seed for the experiments in Hawaii and Peru; we have supplied in vitro cultures for multiplication in Tunisia; and we have provided disease-free tubers for multiplication to the Philippines. A summary of these experiments is listed in Table A.1.

Data from all 12 of these experiments are or will be available to the researchers who have been participating in this BARD project. The data sets will provide a rich resource for model testing and validation. All experiments have had at least three replications, and standardized meteorological data appropriate for crop modeling have been collected and stored in computer format. The 1985 experiment at Cornell is described below.

Table A.1. Summary of replicated growth analysis experiments at various field locations supported totally or in part by the BARD project. Biomass and meteorological data sets for each experiment followed a common plan and included a common set of cultivars.

Location	Cooperating Agency ¹	Year	Conditions	Role of BARD
Cornell	---	1985	Temperate	Full support
Cornell	---	1986	"	" "
Hawaii	IBSNAT	1985	1,097 m elevation	Supplied seed
Hawaii	"	"	282 m elevation	" "
Hawaii	"	"	91 m elevation	" "
Hawaii	"	1986	1,097 m elevation	" "
Hawaii	"	"	282 m elevation	" "
Hawaii	"	"	91 m elevation	" "
Peru	CIP	1986	800 m elevation	" "
Tunisia	USAID	1985	Summer planting	Supplied in vitro plants
Tunisia	"	1986	Summer planting	" "
Philippines	CIP	(To be planted, 1987)		Supplied tubers for multiplication

¹IBSNAT = International Benchmark Sites Network for Agrotechnology Transfer --a US AID project administered through the University of Hawaii. The project in Tunisia is a linkage project with US AID administered through the University of Missouri. CIP = The International Potato Center, Peru.

Materials and Methods. The six cultivars were planted in the field on 15 May 1985. The experimental design was a randomized complete block - split plot, with cultivars serving as the main plots, and harvest dates as the subplots. There were three replications, 18 plots in all. Within each plot, the four rows used for data were bounded by two guard rows of the same cultivar. Both edges of the field were bounded by guard rows of the cultivar Rosa. The data rows consisted of alternating pairs of plants, two for sampling and two for guard plants within each row, so that two plants per row for each of the four rows were sampled on each harvest date. Five Norgold Russet tubers were used to separate plots and to separate the plants for growth analysis from the remainder of the plot used for final yield determination. This latter part consisted of four rows of ten plants each, so that 40 plants per plot could be harvested at the end of the season to evaluate yield and quality.

At planting, whole tubers of 30 - 50 g were hand placed into pre-formed furrows to insure uniform spacing at 25 cm between plants. Rows were spaced at 84 cm. The soil was a Howard gravelly loam. Preemergent herbicide and a systemic insecticide were used to control pests. Periodic foliar applications of recommended insecticide and fungicide were used as needed during the season. Standard fertilization was supplied, and irrigation was applied to maintain adequate soil moisture throughout the season.

A separate part of the field was planted with 45 tubers in a row per cultivar to supply plants for weekly leaf area measurements. Three rows of each cultivar were planted, but sample plants were selected only from the center rows. A Li-Cor wide belt leaf area meter was used. As plants were sampled, two guard plants were left to separate the sample plant from the gap left from the previous week's sample. Thus only every third plant in each sample row was used.

For the first few weeks following planting, daily counts of emergence for each cultivar were recorded, and weekly estimates of percent cover were made until full canopy closure was attained. Harvests for growth analysis were done on 24 June, 29 July, and 28 August. On each harvest date, eight plants were harvested in each of the 18 plots. The number of main stems per plant were counted, and then haulms were severed at the soil line. The tops from six of the eight plants were pooled into one plastic bag for determination of average haulm fresh and dry weights. The remaining two plants were each divided into four sub-sets: main stems, main stem leaves, branch stems, and branch stem leaves. Leaf area from main and branch stems was recorded, and then dry weights for each of these four sub-sets were measured. Tubers from all eight plants were pooled. They were divided into two size classes, 5 to 30 mm and greater than 30 mm in diameter. Number, fresh weight, and percent dry matter of tubers in each size class were measured.

The final harvest for yield and quality of tubers was done on 3 October. Tubers from 40 plants per plot were separated into five size classes, A to E, as follows: <48 mm, 48 to 64 mm, 64 to 83 mm, 83 to 102 mm, and >102 mm in diameter, respectively. They were also graded for internal and external defects, including greening, scab, bruising, hollow heart, stem-end rot, soft rots, and internal discoloration. For internal defects,

10 tubers were selected randomly from the mid to upper size classes. Specific gravity was measured with a potato hydrometer.

A small weather station was installed to monitor total irradiance; air, canopy, and soil temperatures; relative humidity; wind run; and rainfall. The weather data were monitored and recorded hourly during the entire growing season with the use of a Campbell Scientific CR-21 Micrologger.

Results. The curves of cumulative emergence counts followed the sigmoid shape for all cultivars, as expected (Fig. A.1). However, there appeared to be a segregation among cultivars in the steepness of curves. C14-343 began emergence the earliest, at 13 days after planting, and continued to have the highest cumulative emergence number except for Desiree. Desiree did not emerge in significant numbers until 19 days after planting, but then 74% of plants emerged within a 2-day period, making a remarkably uniform emergence. Katahdin and C1-884 were relatively late emerging, not appearing in large numbers until 21 days after planting. Although C1-884 is an early maturing clone, it has a relatively long dormant period, which probably explains the late emergence. Norchip and LT-1 were midway between the cultivars already described. All cultivars were at full emergence 26 days after planting.

Weekly readings of percent cover of each cultivar were recorded to quantify the differences among cultivars in how quickly they fill out the row and reach 100% cover. There were three groups distinguished by the curves of these data (Table A.2). Desiree was clearly the quickest to fill out the row and reach 100% cover. In the second group, LT-1, C1-884, and C14-343 all had similar curves, and reached 100% cover several days later. Norchip and Katahdin were intermediate between these two groups in rate of developing canopy cover.

Table A.2. Percent cover of six cultivars and clones of potato, Freeville, NY. Planted 15 May 1985.

	CULTIVAR					
	NOR	KAT	LT	C1	C14	DES
24 June	40.3	35.0	34.0	37.0	38.7	42.7
2 July	58.3	57.0	52.3	55.3	56.0	65.0
11 July	88.0	87.7	81.7	78.3	79.7	100.
15 July	99.3	100.	93.3	88.0	84.7	100.
18 July	100.	100.	92.0	92.0	92.7	100.
24 July	100.	100.	100.	100.	100.	100.

There were significant differences among cultivars in the number of main stems per plant, but not among harvest dates. Norchip had 3.4 while LT-1 had only 1.8 main stems per plant. The other cultivars had between 2.2 and 2.9 main stems (Table A.3). This was a highly significant difference.

Fig. A.1. Plant emergence of 6 cultivars, planted 15 May 1985 (Julian day 135); number emerged of 138 seed pieces planted.

Table A.3. Influence of cultivar on number of main stems per plant, mean three harvests, 24 plants per harvest¹.

CULTIVAR					
<u>NOR</u>	<u>KAT</u>	<u>LT</u>	<u>C1</u>	<u>C14</u>	<u>DES</u>
3.4	2.9	1.8	2.3	2.2	2.3
a	ab	c	bc	bc	bc

¹ Mean separation by Duncan's New Multiple Range Test.

Means followed by the same letter are not significantly different at $p = 0.05$.

Differences in both fresh and dry weights of above ground plant parts (haulms) were highly significant between cultivars, harvests, and the interaction between the two. The significance of the main effect of cultivar reflected the fact that the late cultivars, Desiree, Katahdin and LT-1, produced a large amount of foliage compared to the early cultivars, C1-884 and Norchip (Fig. A.2). Differences between harvest dates were to be expected. The interaction is a result of C1-884 and C14-343 decreasing in dry weights of haulms in August due to senescence, while the very late cultivar, LT-1, was still increasing in dry weight. Norchip, Katahdin, and Desiree increased by a smaller amount in dry weight of haulms during this period.

Leaf area of main and branch stem leaves was significantly different between cultivars and highly significantly different between harvest dates. The interaction was not significant for either of these dependent variables. Leaf area of main stems was much larger at the July harvest than either the June or August harvest dates (Table A.4). With branch stems, the August leaf area was higher than in either of the preceding two months, with June leaf area negligible (Table A.5). Katahdin had a significantly higher total leaf area on main stems than did C1-884, with the other four cultivars having intermediate values (Table A.6). With branch stems, Norchip had less leaf area than the others, perhaps because this cultivar had more main stems than the other cultivars, so that branch growth was less (Table A.7). Senescence on main stems occurred earlier than on branch stems. Branch leaf area increased after leaf area began to decrease on main stems. This was true with all cultivars tested, except Norchip. In Norchip, about an equal leaf area was found on main and branch stems in August.

For dry weight of main stem leaves, the main effect of harvest date was significant, while both the effect of cultivar and the interaction were very highly significant (Fig. A.2). The harvest effect is due to the rapid increase in dry weight of main stem leaves between the June and July harvests, and then the decrease in dry weight from July to August due to senescence of main stems and leaves. Later cultivars, especially Katahdin and LT-1, produced more total main stem leaf dry weight than the other cultivars. The interaction was due mainly to the distinctive behavior of Norchip. Unlike all other cultivars examined, Norchip dry weight of main

Fig. A.2. Growth analyses of 6 cultivars grown in Freeville, NY in summer, 1985. BL=branch stem leaves, BS=branch stems, ML=main stem leaves, MS=main stems, Harvests: 24 June (J), 29 July (J), and 28 August (A).

N=Norchip, K=Katahdin, L=LT-1, 1=C1-884, 4=C14343, D=Desiree

stem leaves did not increase as sharply from the June to July harvest, and did not drop nearly as much between the July and August harvest dates.

Table A.4. Influence of harvest date on main stem leaf area per plant, mean of six cultivars, six plants per cultivar (cm²)

Harvest Date		
<u>24 June</u>	<u>29 July</u>	<u>28 August</u>
1169	4992	2135

Table A.5. Influence of harvest date on branch stem leaf area per plant, mean of six cultivars, six plants per cultivar (cm²)¹.

Harvest Date		
<u>24 June</u>	<u>29 July</u>	<u>28 August</u>
52	2293	4236

Table A.6. Influence of cultivar on main stem leaf area per plant, mean of three harvests, six plants per harvest (cm²)¹.

CULTIVAR					
<u>NOR</u>	<u>KAT</u>	<u>LT</u>	<u>C1</u>	<u>C14</u>	<u>DES</u>
2914 ab	3522 a	3219 ab	2032 b	2309 ab	2595 ab

¹ Mean separation by Duncan's New Multiple Range Test.
Means followed by the same letter are not significantly different at $p = 0.05$.

Table A.7. Influence of cultivar on branch stem leaf area per plant, means of three harvests, six plants per harvest (cm^2)¹.

CULTIVAR					
NOR	KAT	LT	C1	C14	DES
1023	2758	2803	1353	2069	3155
n.s.					

¹ Mean separation by Duncan's New Multiple Range Test.
 Means are not significantly different at $p = 0.05$.

Significant differences with branch stem leaves were similar to those of main stem leaves, but the shape of the curves was very different (Fig. A.2). While main stem leaf dry weights decreased from mid to late season, branch stem leaf dry weights continued to increase. This pattern explains the significance of the harvest date effects. The increase in dry weight over all three harvests is true for all cultivars except C1-884, the earliest cultivar of this set. C1-884 actually dropped off slightly in dry weight of branch stem leaves after the July harvest. This is the most conspicuous reason for the significant interaction. In addition, Norchip and C14-343 did not increase in dry weight as much as Desiree, Katahdin, and especially LT-1. The slope of increase in branch stem leaf dry weight of Norchip was also less than the other four cultivars throughout the season.

Both main effects and interactions caused highly significant differences in the dry weights of main stems (Fig. A.2). The effect of cultivar is due to the late cultivars (LT-1, Katahdin, and Desiree) accumulating more dry weight than the earlier cultivars, especially noticeable at the July harvest. Harvest effects are due to the same trend observed with main stem leaves: a large increase in dry matter from the first to second harvest dates. But unlike main stem leaves, the dry weights of main stems of LT-1, Katahdin, and Norchip did not decrease from July to August (Fig. A.2). However, Desiree and the two Neo-tuberosum clones did decrease in dry weight due to senescence.

Similar findings of highly significant effects were noted with branch stem dry weights (Fig. A.2). Varietal and harvest date main effects can be explained the same way as with the main stems. As with branch stem leaves, the dry weight of branch stems tended to increase from June to August for LT-1, Desiree, Katahdin, and C14-343. Only the earliest cultivars, C1-884 and Norchip, had little change throughout this period (Fig. A.2). This explains the significant interaction.

For fresh weight of small tubers (5 - 30 mm diameter), means of main effects and the interaction were significantly different. As would be expected, harvest date was significant since most of the dry weight of tubers in this small size class occurred during July, while little or none appeared in June (Table A.8). Only the late cultivars Katahdin and LT-1 produced no tubers by 24 June, accounting in part for the significant

interaction. By the time of the August harvest, most of these small tubers had either been resorbed or grown into larger tubers; so the total dry weights of small tubers dropped again in August for every cultivar except Desiree, which showed little change.

Table A.8. Influence of cultivar and harvest date on fresh weight of tubers 5 - 30 mm diameter, sum of eight plants (g)¹.

HARVEST	CULTIVAR					
	NOR	KAT	LT	C1	C14	DES
24 JUNE	8	0	0	2	10	4 n.s.
29 JULY	132 ab	87 abc	73 bc	77 bc	167 a	25 c
28 AUGUST	28	72	37	43	67	27 n.s.

¹ Mean separation within rows by Duncan's New Multiple Range Test.
Means followed by the same letter are not significantly different at $p = 0.05$.

For fresh weight of tubers > 30 mm diameter, again both main effects and the interaction were significant. There were no large (greater than 30 mm) tubers formed by the time of the 24 June harvest in any cultivar. Production of large tuber dry weight was higher in August than in July, since many of the tubers that were still small in July entered this larger size class during August (Table A.9). C1-884, Norchip, and Katahdin all had similar, high yields of tubers in this size class, while LT-1 had a much lower yield. The relative total yields of the six cultivars can be seen in Fig. A.2, expressed as dry weights.

Table A.9. Influence of cultivar and harvest date on fresh weight of tubers > 30 mm diameter, sum of eight plants (g)¹.

HARVEST	CULTIVAR					
	NOR	KAT	LT	C1	C14	DES
24 JUNE	0	0	0	0	0	0 n.s.
29 JULY	4088 ab	3118 ab	2332 b	4683 a	3463 ab	4502 ab
28 AUGUST	9575 a	8663 a	6143 b	9417 a	8080 ab	9312 a

¹ Mean separation within rows by Duncan's New Multiple Range Test.
Means followed by the same letter are not significantly different at $p = 0.05$.

At final harvest on 3 October, Desiree had the highest total yield, followed closely by Katahdin, and then C1-884 (Table A.10). These were in the range of 1080 to 1210 g/plant. LT-1 and Norchip had much lower yields, 790 to 830 g/plant. There were significant differences in each of the five size classes evaluated. The relative fresh weights of tubers in each size class are depicted in Figure A.3. C14-343 had the largest portion of small tubers, making up the first two size classes (less than 64 mm diameter). On the other hand, only Katahdin and LT-1 produced any tubers in the largest size class (greater than 102 mm diameter). There will be some degree of bias against Desiree in measuring size distribution, since it is an elongated cultivar, and the tubers were sized on a mechanical grading table.

Although Katahdin and Desiree had the highest total yield, they also had the highest fresh weights of tubers with grade defects (Table A.10), primarily misshapen tubers with Desiree and green tubers with Katahdin. LT-1 also had a high level of defects, about equally divided between green and misshapen tubers. The low occurrence of green potatoes in Desiree could be partly due to the red skin color masking its appearance. There were no significant differences among cultivars in the incidence of scab, hollow heart, stem-end rot, or soft rots. Occurrence of these defects was very low except for scab. LT-1 had the worst rating for scab, although it was not significantly different from the other cultivars. C1-884 had very low levels of defects, and had the lowest fresh weight of misshapen tubers. In a more subjective rating, C1-884 had the best overall appearance, while LT-1 had the least desirable appearance. C1-884, which had a slightly lower total yield than Desiree and Katahdin, had the lowest weights of tubers with defects and had the highest yield of % U.S. No. 1 quality potatoes (97%) (Table A.10).

Table A.10. Influence of cultivar on fresh weight yield, quality, and specific gravity of a potato crop, Freeville, NY, 3 October, 1986 (means of three replications)¹.

	CULTIVAR					
	<u>NOR</u>	<u>KAT</u>	<u>LT</u>	<u>C1</u>	<u>C14</u>	<u>DES</u>
Total Yield (g/plant)	788 b	1130 a	826 b	1080 ab	991 ab	1210 a
Total Yield (t/ha)	3.8 b	5.4 a	3.9 b	5.1 ab	4.7 ab	5.8 a
% U.S. No. 1	77 cd	86 b	76 cd	97 a	82 bc	73 d
US No. 1 Yield (t/ha)	2.9 b	4.6 ab	3.0 ab	5.0 a	3.9 ab	4.2 ab
Specific Gravity	1.090 b	1.084 b	1.098 a	1.085 b	1.083 b	1.089 b

¹ Mean separation within rows by Duncan's New Multiple Range Test. Means followed by same letter are not significantly different at $p = 0.05$.

Fig. A.3. Tuber size distribution from final harvest of potato crop grown in Freeville, NY, summer, 1985 (size classes indicated in mm).

The differences among cultivars for specific gravity were highly significant. LT-1 had the highest average specific gravity at 1.098 (Table A.10). Specific gravities of the other cultivars were lower, but within the range generally considered very acceptable.

Discussion. Emergence rates were not determined by earliness of cultivars and clones. C14-343 emerged first, and had higher cumulative emergence numbers until surpassed by Desiree. Although Desiree was not an early emerger, this cultivar had extremely uniform emergence, with 74% of plants emerging within a 2-day period. Desiree was also the quickest at filling out the row with foliage to provide 100% cover.

It is believed that cultivars which possess the ability to fill out the row quickly may be more suitable for the hot tropics than other cultivars because they will shade the soil earlier, lowering soil temperature (Midmore, 1984; Midmore and Mendoza, 1984). Cooler soil temperature in the tropics has been associated with improved yields (Manrique and Meyer, 1984). In addition, even in the temperate zone, cultivars which reach 100% cover quickly are preferred, since the dense shade that they produce helps to control weeds; also yields are likely to be higher, since full cover for a longer period permits a greater conversion of radiant energy into biomass (Van der Zaag, 1984).

All cultivars except Norchip and Katahdin had about two main stems per plant. Norchip averaged 3.4, while Katahdin had 2.9. Late cultivars produced more foliage than early cultivars, especially later in the season. It is not too surprising that the late cultivars LT-1 and Katahdin did not senesce by the August harvest, or that the earlier cultivars C1-884 and C14-343 did senesce; but it was unexpected that Norchip, an early cultivar, was still increasing in dry weight of main stems in August.

An interesting trend was noted in leaf and stem dry weights. Main stem leaf and stem dry weights tended to decrease earlier in the season than total above ground dry weight would indicate, especially in the late cultivars. This is because the larger share of above ground dry weight was taken over by increases in branch leaf and stem growth as main stem parts senesced. Considering both leaf and stem dry weights, the early cultivars consisted mostly of main stem growth, and the branch system remained limited.

Total tuber yield was highest with Desiree, followed very closely by Katahdin and C1-884. However, since C1-884 had a very low percentage of defects, it had the highest yield of U.S. No. 1 quality potatoes, with 97%. In regards to size distribution, LT-1 had a lower yield of large tubers in August. This is because it is an extremely late cultivar and would, therefore, produce more dry matter after the August harvest than would the other cultivars. It was interesting that C1-884 produced so well in this large size range, since it is a very early cultivar and had less haulm growth and total leaf area than the other cultivars. LT-1 was the poorest yielder, probably because under long photoperiods it requires a longer season than is available in New York State. Thus C1-884 and LT-1 represent opposite poles in ability to partition dry matter to tubers, at least under temperate conditions, even though both have performed well in the warm tropics.

2. Greenhouse experiments

Experiment a.

The six cultivars and clones were grown in both a hot and an ambient temperature greenhouse. Cultural methods and design in the two greenhouses were identical except for temperature. Since there were no replications of the temperature treatments, i.e. only one hot and one ambient greenhouse, no statistical comparisons were made between the two temperatures.

Materials and Methods. Plants were grown in 20-cm clay pots filled with Cornell Peat-Lite mix (Boodley and Sheldrake, 1973), with each plant serving as an experimental unit. The greenhouse was blocked longitudinally into three long strips for temperature effects within the greenhouse due to location. All cultivars were present in each block, and the location of cultivars within blocks was randomized. However, blocks of each cultivar were contiguous, i.e. on the same bench. There were three harvest dates, with three plants of each cultivar and location harvested per date. Therefore, there were 27 plants of each cultivar in each of the two greenhouses, 324 plants in total. The experimental design was a randomized complete block - split plot, with main plots of cultivar and location (within the greenhouse) and a subplot of harvest date.

Cut pre-sprouted tubers were planted on 18 May 1984. All but one sprout per seed piece was removed so there would be only one main stem per plant. Furthermore, after emergence plants were again thinned to one main stem as often as needed. Plants for both greenhouses were grown under ambient temperature in the same greenhouse until the beginning of the heat treatment on 8 June, when half of the plants were moved into the hot greenhouse. A trickle irrigation system (Chapin Watermatics) was installed in both greenhouses to facilitate watering, especially in the hot greenhouse. Irrigation was controlled by time clocks and solenoids, and was increased in volume as needed depending on plant size. Standard fertilization and control of greenhouse insects and diseases were used. Plants were held erect with bamboo stakes and tied to stakes periodically. The temperature in the ambient greenhouse was maintained as close to ambient as possible by installing a mesh fabric along the side walls, and ventilating with exhaust fans as needed. A thermostat in the hot greenhouse was set to activate supplemental heating at 36 C for days and 32 C for nights. Although exhaust fans were activated when temperature rose above 38 C, on sunny days temperature often continued to rise to over 43 C. The photoperiod in both houses was extended to 18 hours with the use of 50-W incandescent lamps controlled by time clocks.

Destructive harvest of plants was done on 18 July, 15 August, and 11 September. Before harvesting, the height of each plant was recorded. Height was measured from the soil line to apex of each plant, excluding inflorescence. Stem diameter, recorded only after the August harvest, was measured at the soil line. Plants were cut at the soil line, and leaves were separated from stems. Leaf area for each plant was recorded after the first harvest, but for only one plant per cultivar and location after the second and third harvest dates, using a Li-Cor wide belt Leaf Area Meter. Tubers from each pot were counted and fresh weights determined. Then they were cut with a french fry cutter and put into drying ovens. Dry weights of

leaves and stems were determined after drying for four days and tubers after seven days in 70 C drying ovens. Just before the final harvest date, numerical ratings for vigor and senescence were assigned using 1 to 9 scales, with 9 being the most vigorous and least senescent, respectively.

Results.

1) Ambient Greenhouse

Significant differences in plant height were found among cultivars, among harvest dates, for the 2-way interaction of harvest date times cultivar, and for the 3-way interaction of harvest, cultivar, and location within the greenhouse. There was no significant main effect of location, or the interaction of location with harvest date. The main effects of harvest date and cultivar are expected, due to genetic differences and growth over time. The very late clone, LT-1, and Desiree were taller than the early C1-884 and Norchip, with the other two cultivars reaching intermediate heights (Table A.11). The interaction of harvest date and cultivar can be explained by the fact that C14-343, C1-884, and Desiree had about the same rate of change in height from July to August as from August to September. However, the other cultivars, especially Katahdin, had a much greater increase in height between the first two dates than between the second two (Table A.11).

Table A.11. Influence of cultivar and harvest date on plant height in the ambient and hot greenhouses. Data (cm) are means of nine plants, except as noted¹.

<u>HARVEST</u>	<u>CULTIVAR</u>					
	<u>NOR</u>	<u>KAT</u>	<u>LT</u>	<u>C1</u>	<u>C14</u>	<u>DES</u>
AMBIENT GH						
18 JULY	64 c	83 b	81 b	61 c	88 ab	101 a
15 AUG	87 c	131 a	129 a	75 c	104 b	141 a
11 SEPT	88 d	135 b	154 a	76 d	115 c	168 a
HOT GH						
18 JULY	57 ab	63 ab	51 b	70 a	68 a	50 b
15 AUG	77 b	72 b	67*c	84 ab	94 a	86 ab
11 SEPT	91 b	100 b	**	85 b	129 a	119 a

* mean of six surviving plants.

** all plants of LT-1 were dead by 11 Sept.

¹ Mean separation within rows by Duncan's New Multiple Range Test. Means followed by the same letter are not significantly different at $p = 0.05$.

Leaf dry weight was significantly different for the main effects of cultivar and harvest date, and for the interaction between these factors. The explanation of main effects for plant height also applies to dry weight of leaves. The later cultivars again had the highest dry weight, while the early cultivars, plus C14-343, had lower dry weights (Fig. A.4). The interaction is also associated with differences in maturity. LT-1 and Desiree continued to increase in dry weight, while the other four cultivars dropped in dry weight from the August to the September harvest dates. C1-884, the earliest cultivar, had the lowest dry weight of leaves throughout the experiment and also senesced the most between the second and third harvest dates (Fig. A.4).

Significance of differences in dry weight of stems was the same as with leaves. Again, the late cultivars LT-1 and Desiree had higher dry weights, while the earlier cultivars, C1-884 and Norchip, were lower in dry weight (Fig. A.4). The interaction of cultivar and harvest date is also a product of maturity; early cultivars had less stem growth between August and September than did late cultivars, although stem dry weights still increased during this time (Fig. A.4). There is question as to whether stem samples were adequately oven-dried for the July harvest, so these were excluded from the analysis of variance and are not presented.

Since effects were similar for fresh weights and dry weights of tubers, only dry weights will be discussed. Tubers differed in the main effects of cultivar and harvest date, and in the interactions of harvest and cultivar, and harvest and location. Although all cultivars increased in dry matter of tubers with time, the early cultivars C1-884 and Norchip had higher dry weights at the first harvest, and maintained higher dry weights at the August harvest (Fig. A.4). On the other hand, LT-1 had lower dry weight of tubers throughout the season. Katahdin and C14-343 had a higher rate of tuber dry weight increase between August and September than did the other cultivars, especially LT-1, explaining the interaction. By the September harvest, Katahdin had the highest dry weight (Fig. A.4).

There were significant differences in tuber numbers due to cultivar, harvest date, and their interaction. Unlike dry weights of leaves, stems, and tubers, the differences in the number of tubers were not segregated between early vs. late cultivars. Desiree and C14-343 had the most tubers, while Katahdin had the fewest (Table A.12). Since Katahdin had the highest dry weight but the lowest number of tubers by the end of the season, it is evident that Katahdin produced the largest tubers. On the other hand, the large number of Desiree tubers shows that this cultivar produced many smaller tubers, compared to the other cultivars. The significant interaction is due mainly to the cultivars Desiree, C14-343, and LT-1 increasing in number of tubers more between August and September than the other cultivars did. By September, the other cultivars were primarily increasing in dry weights of tubers rather than initiating new ones.

Stem diameter was measured only on 11 September, before the last harvest. There were highly significant differences between cultivars. Desiree and LT-1 had the largest diameter, 12 mm, while C1-884 had the smallest, 8 mm (Table A.13). Stem diameter, apparently, is not correlated with yield in the ambient greenhouse.

Fig. A.4. Growth analyses of 6 cultivars in ambient temperature greenhouse; August (A) and September (S) harvests for stems, stems + leaves, and tuber dry weights shown. Tubers are plotted below the abscissa. N=Norchip, K=Katahdin, L=LT-1, l=C1-884, 4=C14-343, D=Desiree; T=Tuber dry weight, S=Stem dry weight, L+S=Leaf + Stem Dry weights.

Table A.12. Influence of cultivar and harvest date on number of tubers, mean of nine plants, except as noted¹.

HARVEST	CULTIVAR					
	NOR	KAT	LT	C1	C14	DES
AMBIENT GH						
18 JULY	7	6	4	8	8	7 n.s.
15 AUG	9 ab	7 b	7 b	11 ab	13 a	11 ab
11 SEPT	9 cd	6 d	11 c	12 c	17 b	22 a
HOT GH						
18 JULY	0	0	0	2	2	0 n.s.
15 AUG	1 b	0 b	0*b	6 a	3 ab	0 b
11 SEPT	6 b	0 c	**	4 bc	17 a	1 c

* mean of surviving six plants

** all plants of LT-1 were dead by 11 Sept.

¹ Mean separation within rows by Duncan's New Multiple Range Test.
Means followed by the same letter are not significantly different
at $p = 0.05$.

Table A.13. Influence of cultivar on stem diameter on 11 September, mean of nine plants (mm)¹.

	CULTIVAR					
	NOR	KAT	LT	C1	C14	DES
AMBIENT GH	10	11	12	8	9	12 n.s.
HOT GH	13	12	*	8	10	13 n.s.

* all plants of LT-1 were dead by 11 Sept.

¹ Mean separation within rows by Duncan's New Multiple Range Test.
Means followed by the same letter are not significantly different
at $p = 0.05$.

2) Hot Greenhouse

The heights of plants in the hot greenhouse were significantly different between the main plots of cultivar and harvest date, and in the interactions of cultivar and location, cultivar and harvest, and the three way interaction (Table A.11). Significance due to the cultivars or to interactions with cultivars are mainly due to the mortality of LT-1 plants. At the August harvest, the mean of the heights of the surviving six LT-1 plants was less than the means of the other cultivars, and by September, all plants had died. Statistical analysis for this and other variables was done using missing plots for the August harvest, while for the September data, LT-1 was not included. Although LT-1 is known to possess heat tolerance under field conditions in the lowland tropics, the temperature regime in the hot greenhouse is much more severe. Except for LT-1, the mid and late season cultivars C14-343, Desiree, and Katahdin were taller in the hot greenhouse than the earlier cultivars. Also, the early cultivars did not change much in height between August and September.

The same factors and interactions that were significant for height were also significant for dry weight of leaves (Fig. A.5). The death of LT-1 plants played a similar role in this dependent variable. Norchip had higher dry weight of leaves throughout the season, but especially by the September harvest. The other cultivars were very close in leaf dry weight throughout the season. For all cultivars except LT-1 leaf dry weights continued to increase up to the September harvest, indicating delayed senescence from the very high temperatures.

Stem dry weight was also significantly different for the same factors and interactions as the last two variables (Fig. A.5). The effect of the death of LT-1 plants was again evident. Other than this primary cause of the significance of interactions involving cultivar, it is noted that C1-884 and Katahdin did not increase in stem dry weight between August and September as much as the other three cultivars (Fig. A.5).

For tuber dry weight, cultivars, harvest dates, and the interaction between these two main effects were all significantly different (Fig. A.5). The differences among cultivars were pronounced. LT-1 and Katahdin produced virtually no tuber dry weight. Desiree, C1-884, and Norchip all yielded under 20 g of tuber dry weight per plant, a very small yield. However, C14-343 produced 57 g of dry weight per plant. Although this is still a very small yield compared to yields of approximately 200 g per plant in the ambient greenhouse, it is far better than yields of the other cultivars in the hot greenhouse (Fig. A.5).

Cultivars, harvest date, and their interaction were also significantly different for tuber number (Table A.12). All cultivars except C14-343 had fewer than six tubers per plant, with none produced by LT-1; whereas C14-343 had an average of 17 tubers per plant in the hot greenhouse. Tubers produced by all five cultivars were very small, between 2.7 and 4.6 g dry weight each.

Stem diameter was measured once, on 11 September, before the last harvest (Table A.13). There were significant differences among cultivars. Norchip and Desiree had the greatest stem diameter, 13 mm, while C1-884 had

Fig. A.5. Growth analyses of 6 cultivars in hot temperature greenhouse; July, August, and September harvests for stems, stems + leaves, and tuber dry weights shown. Tubers are plotted below the abscissa. J=July, A=August, S=September harvests: N=Norchip, K=Katahdin, L=LT-1, 1=C1-884, 4=C14-343, D=Desiree.

the smallest, at 8 mm. This is similar to the ambient greenhouse, in which Desiree had the largest diameter and C1-884 the smallest. Since no plants of LT-1 survived to this date, there are no data for this clone.

Discussion. Much of the growth pattern of these six cultivars in the ambient greenhouse can be explained in terms of whether they tend to be early or late in maturity. In the ambient greenhouse plant height and dry weights of leaves and stems did not increase as much between August and September for the earlier cultivars as for the later ones. Dry weights of leaves decreased for this period for all except LT-1 and Desiree.

In the heat stressed conditions of the hot greenhouse, these patterns broke down for dry weights. Norchip had higher leaf dry weight throughout the season in the hot greenhouse but especially at the September harvest. Plant height ranking was similar in the ambient and hot greenhouses, with the later cultivars tending to be taller than the earlier ones. The exception was with LT-1, which did not survive well in the hot greenhouse.

The ranking of tuber dry weight production in the ambient greenhouse was according to earliness, with the early cultivars C1-884 and Norchip having highest early yields. Except for the very late LT-1, the other cultivars caught up with the early ones by the final tuber harvest. However, in the hot greenhouse LT-1 produced no yield, and Katahdin and Desiree almost none, even by the final harvest. The very early cultivars were better than the late ones, although the best tuber yield was from the moderately late C14-343, which gave about one-fourth of the yield it produced in the cooler greenhouse.

It should be emphasized that the environment in the hot greenhouse was more severe than in the lowland tropics. LT-1 has been shown to be tolerant of high temperature in the field at San Ramon, Peru (elevation, 800 m; 11 degrees South), and at various other sub-tropical and tropical locations. Not only was the temperature in the greenhouse over 38 C on sunny days, but the photoperiod was extended to 18 hours. Other research has shown that with the photoperiod extended to 16 hours, tuberization on cuttings of LT-1 was substantially reduced, even with cool temperature (see Part E 1, below). Therefore, performance in the hot greenhouse cannot be directly extrapolated to field conditions in hot climates.

Experiment b.

A growth analysis was carried out in hot and control greenhouses at Rehovot during the summer of 1986.

Materials and Methods. Tubers of six varieties (C1-884, C14-343, LT-1, Norchip, Up-to-Date and Desiree) were planted in the two greenhouses on 15.4.86. Maximum temperature was 25 C in both treatments until emergence. After emergence, air temperature in the ambient greenhouse was about 2 degrees C above the outside temperature during the day (31-33 C), and about the same temperature as the outside temperature during the night (19-21 C). The temperature in the hot greenhouse was 38-42 C during most of the day, and similar to the outside temperature during the night. Unfortunately, temperature regimes in the control greenhouse were higher than the optimum temperatures for tuber production.

Results and Discussion. The effect of the high temperature treatment on total biomass depended upon the variety. Extra heat stress caused a reduction of total dry weight of C14-343, LT-1, and Norchip; but no significant reduction was observed in C1-884, Up-to-Date, or Desiree (Fig. A.6, A.7, A.8, A.9, A.10, A.11). Shoot growth of all varieties was faster under the high temperature conditions, and there was a reduction of dry weight partitioning to the tubers; but varieties differed in the degree to which they were affected (Figs. A.6, A.7, A.8, A.9, A.10, A.11). Up-to-Date was the most sensitive variety to high temperatures, in spite of the fact that high temperatures did not cause a reduction of total biomass. C14-343, C1-884, and Norchip displayed an ability to tuberize under the hot treatment as well. Thus the results were in good agreement with the greenhouse experiment at Cornell.

B. Time and Method of Heat Stress

1. Stage of growth at heat stress (Phytotron experiment, Israel)

This was a study of the effect of heat stress at different stages of plant development on dry matter partitioning to plant organs and on tuber yields. The experiment was carried out in the phytotron at day/night temperatures of 27/12 C (normal temperatures) and 32/27 C (heat treatment), with a photoperiod of 16 hours. Two potato varieties, Desiree and Alpha, were grown in 20-cm black pots from single rooted stems.

Materials and Methods. Heat treatment was applied at three consecutive 2-week intervals, denoted as stages 1 to 3. Plants were returned to the normal temperature after each treatment. The first treatment was initiated at the 3 to 4 leaf stage of plant development. Two control groups consisted of plants which were grown at 27/12 C and 32/27 C, respectively, for the entire 6-week duration of the experiment. Fresh and dry weights of the different organs as well as other plant parameters were measured at the end of the experiment. Dry weight results are expressed as the percent of dry weight in each plant organ out of the total plant dry weight.

Results and Discussion. No significant differences were found in total dry weight per plant between the treatments (Fig. B.1). Significant differences between treatments, however, were found in dry weights of stems and leaves, which were significantly greater in the continuously hot control, and in the second stage treatment (Figs. B.2, B.3).

Dry weight of tubers was significantly lower in the continuously hot control and in the second stage treatment (Fig. B.4). Dry weight partitioning to the roots was also affected by heat treatment. A significantly higher partitioning to roots occurred in the continuously hot control (Fig. B.5).

Heat treatment resulted in a decrease in the number of tubers per plant of Desiree, which is an earlier variety than Alpha. Heat stress at the second stage had the same effect (Fig. B.6). This decrease was largely due to an interference with tuber initiation. No significant differences in

Fig. A.6. Dry weight partitioning, Greenhouse, 1986

25

a. C1-884 - hot treatment

b. C1-884 - control

Fig. A.7. Dry weight partitioning, Greenhouse, 1986.
a. C14-343 - hot treatment.

26

b. C14-343 - control.

Fig. A.8. Dry weight partitioning, Greenhouse, 1986.
a. LT-1 - hot treatment.

27

b. LT-1 - control.

Fig. A.9. Dry weight partitioning, Greenhouse, 1986.
a. Norchip - hot treatment.

28

b. Norchip - control.

a. Up-to-Date - hot treatment.

b. Up-to-Date - control.

Fig. A.11. Dry weight partitioning, Greenhouse, 1986.

a. Désirée - hot treatment

b. Désirée - control.

Fig. B.1. Total dry weight of plants from two cultivars grown in the phytotron in Israel under five temperature regimes. Temperatures were elevated to 32/27 C (day/night) for 2 weeks starting 0, 2, or 4 weeks after plants had 3-4 leaves, respectively, for stages 1, 2, and 3. Control treatments received 27/12 C or 32/27 C.

Fig.B.2. Percentage of dry matter partitioned to leaves in the experiment described in Fig. B.1.

Fig. B.3. Percentage of dry matter partitioned to stems in the experiment described in Fig. B.1.

Fig.B.4. Percentage of dry matter partitioned to tubers in the experiment described in Fig. B.1.

Fig.B.5. Percentage of dry matter partitioned to roots in the experiment described in Fig. B.1.

Fig.B.6. Total number of tubers in the experiment described in Fig. B.1.

tuber number were found for Alpha. The Alpha tuber yield, however, was significantly smaller in the continuously hot control and in the second stage treatment (Fig. B.4). This reduction can be attributed to the sensitivity to high temperatures of tuber initiation in Alpha, thus postponing tuber initiation. It can also be a result of a reduction in tuber growth due to high temperature regimes.

2. Effect of night temperature on final organ dry weight (Phytotron experiment, Israel)

Plant growth and development were affected by night temperatures. Total biomass decreased significantly with increasing night temperatures (Table B.1). It appears that the range of 22 C to 27 C had a greater effect than the range between 12 C and 22 C. The final organ weight is a result of dry weight partitioning to the various parts of the plant. The main effect is expressed in the tuber dry weight, which was 5.4 grams at 27 C night temperature as compared to 14.8 grams at 12 C. When data are expressed as percentage of the total plant dry weight, 44% of the dry weight is located in the tubers when night temperatures were high, as compared to 70% for cool nights.

Specific leaf area is a common parameter used in crop simulation models. Higher night temperatures were accompanied by higher values of specific leaf area (Table B.2). Total leaf area was not affected by night temperature, but the total number of leaflets was significantly higher in plants which were maintained at the high temperature regimes. This is a result of increasing the number of leaves and the number of leaflets per leaf (Table B.3).

3. Day temperature x daylength (Phytotron experiment, Israel)

The effect of high temperatures during the day were similar to the effect of high night temperature: a decrease in the total biomass, mainly due to reduction in tuber dry weight (Table B.4). Under both short days and long days, high temperatures reduced the partitioning of dry matter to the tubers and increased the percentage located in the leaves and stems (Table B.5). An interaction was found between the effects of daylengths and temperatures. The effect of daylength on plant growth was pronounced only under high temperature regimes. This is expressed mainly by increasing length of stems and tuber formation under long photoperiod. No effect of long days under moderate day temperature (27 C) was observed (Table B.6).

4. Cultivar x daylength x temperature (Phytotron experiment, Israel)

This was a study of the effect of different day and night temperatures at two daylengths, on growth and tuber production of five potato varieties. Plants were grown in 20-cm black pots from single rooted stems in the phytotron. Temperature regimes were 27/12, 27/22, and 32/22 C (day/night). Daylengths were 8 and 16 hours. During the long days, 12-13 hours were under sun light, and the additional 3-4 hours were from dim lights. Temperature and daylength regimes started when plants had 3-4 leaves. Fresh and dry weights of the different organs were measured six weeks later.

Table B.1 Effects of night temperature on dry weights of various plant organs, cultivar Desiree.

All plants were maintained at day temperatures of 27°C. Photoperiods were 8-h.

Night temperatures °C	Leaves	Stems	Roots	Tubers	Total
12	4.20	1.38 b	0.73	14.78 a	21.11 a
22	3.70	1.38 b	0.78	10.43 b	16.31 ab
27	3.50	1.97 a	0.98	5.42 c	11.45 b
F. values	N.S.	6.49**	N.S.	15.395**	7.65**
S.E. of the mean	N.S.	0.1329	N.S.	1.193	1.65

Table B.2. Effect of night temperature on the relationship between leaf area and leaf weight.

Y = leaf area in m^2

x = gr (specific leaf area is in $\frac{m^2}{gr}$)

1) Fresh weight

Treatment

27/12	$Y = 0.0041 + 0.00276X$
F = 320.91	$r^2 = 0.978$
27/22°C	$Y = -0.0033 + 0.00312X$
F = 515	$r^2 = 0.968$
27/27	$Y = -0.0170 + 0.0034X$
F = 218	$r^2 = 0.968$

2) Dry weight

27/12	$Y = 0.014 + 0.0163X$
F = 106	$r^2 = 0.938$
27/22	$Y = 0.0047 + 0.0243X$
F = 369	$r^2 = 0.982$
27/27	$Y = -0.0522 + 0.0427X$
F = 24.95	$r^2 = 0.780$

Table B.3. Effect of night temperature on the development of potato plants, cultivar Desiree.

Day temperature was 27°C, photoperiods were 8-h.

Night temperature °C	No. of leaves	No. of leaflets	No. of leaflets per leaf	Leaflets area (cm)	Length of stem (cm)	No. of tubers
12	13.89	118.4 b	8.52	722.8	28.51 c	7.66
22	15.33	136.8 ab	9.27	797.2	46.53 b	7.77
27	16.89	154.6 a	9.18	707.2	56.27 a	9.11
F. values	N.S.	4.348 [*]	N.S.	N.S.	32.056 [*]	N.S.
S.E. of the mean	N.S.	8.66	N.S.		2.487	

Table B.4. The effect of day temperature and day length on dry weight accumulation in plant organs, cultivar Desiree. Night temperatures were 22°C.

Temperatures °C	Day length (h)	Leaves	Stems	Tubers	Total
27	8	1.14	0.42 b y	2.59	4.16
27	16	1.70	2.36 a x	0.74	4.80
32	8	1.57	1.05 x	1.32	3.95
32	16	1.72	1.44 y	0.02	3.18
27°C	-	1.42	1.39	1.66 x	4.48 x
32°C	-	1.64	1.24	0.67 y	3.56 y
8 h	-	1.35	0.74 b	1.95 b	4.05
16 h	-	1.71	1.90 a	0.38 a	3.99
S.E. temperature	-	N.S.	N.S.	17.783**	5.768*
S.E. hours	-	N.S.	68.273**	44.818**	N.S.
S.E. interaction	-	N.S.	30.37**	N.S.	N.S.

a, b denote multiple range test between day length;
 x, y denote multiple range test between temperatures.

Table B.5. Effects of day temperatures and lengths on partitioning of dry matter among plant organs. Night temperatures were 22°C.

Temperatures °C	Day length (h)	Leaves	Stems	Tubers
27	8	27.50	10.09 b y	62.41
27	16	35.44	49.83 a	14.73
32	8	40.49	27.88 b x	31.03
32	16	54.88	44.43 a	0.68
27°C	-	31.47 y	29.96 y	38.57 x
32°C	-	47.69 x	36.15 x	16.16 y
8 h	-	33.99 b	18.99 b	47.02 a
16 h	-	45.16 a	47.13 a	7.70 b
S.E. temperatures	-	31.824 ^{**}	5.248 [*]	36.622 ^{**}
S.E. hours	-	15.101 ^{**}	108.49 ^{**}	112.744 ^{**}
S.E. interaction	-	N.S.	18.418 ^{**}	N.S.

a, b denote multiple range test between day length;

x, y denote multiple range test between temperatures.

Table B.6. Effects of day temperatures and day lengths on plant development.

Night temperature was 22°C.

Temperatures °C	Day length (h)	length of main stem (cm)	No. of leaves	No. of tubers	length of internode (cm)
27	8	51.4 b y	13.8	2.8	3.73 b
27	16	83.4 a x	14.4	2.4 x	6.00 a x
32	8	62.6 x	16.4	2.8 a	3.82
32	16	67.4 y	15.6	0.2 b y	4.37 y
27 ⁰	-	67.4	14.1 y	2.6 x	4.86
32 ⁰	-	65.0	16.0 x	1.5 y	4.09
8 h	-	57.0 b	15.1	2.8 a	3.77 b
16 h	-	75.0 a	15.0	1.3 b	5.18 a
S.E. temperatures	-	N.S.	5.121 [*]	4.939 [*]	N.S.
S.E. hours	-	42.533 ^{**}	N.S.	9.184 ^{**}	14.468 ^{**}
S.E. interaction	-	23.236 ^{**}	N.S.	4.939 [*]	5.355 [*]

a,b denote multiple range test between day length;

x,y denote multiple range test between temperatures.

Long days caused a higher total dry weight of all varieties. This result is assumed to be a function of longer days with effective photosynthetic light. There was not a significant effect of temperature regimes on total dry weight of the different varieties (Fig. B.7). Long days and high temperatures caused higher dry matter partitioning to leaves and stems. The temperature effect on stem dry weight was much stronger under long days (Figs. B.8, B.9).

An interaction between the effect of daylengths and temperatures on partitioning to the tubers was observed in this experiment as well (Fig. B.10). Tuber dry weight was very much reduced under long days and high temperatures. Norchip was the least sensitive to high temperatures under short and long days. Desiree was sensitive under both photoperiods, while Alpha, Katahdin and LT-1 were sensitive to heat only under long days. LT-1 is known to be heat tolerant in the lowland tropics under 12 hour photoperiods. This variety was the most sensitive to long days. Even long days under cool temperatures caused a remarkable reduction in dry weight partitioning to the tubers.

5. Soil temperature (Greenhouse and Growth Chambers, Cornell)

These experiments were designed to see whether high air temperatures or high soil temperatures had greater effects on tuberization. Treatments were examined to see whether leaves became induced to tuberize, and, if so, whether the induction in the leaves was expressed underground by production of tubers.

Experiment a.

Materials and Methods. Plants were grown from tubers in pots under favorable conditions for three weeks. They were then transferred to the hot greenhouse (40 C day, 30 C night, 18-h photoperiod). Each plant was grown in a styrofoam pot, 19 cm in diameter, containing coiled copper tubing. For half of the plants, cool water was circulated through the copper tubing. For these plants, daily soil temperatures fluctuated between 23 and 27 C throughout the rest of the season. Daily soil temperatures in the remaining pots varied between 30 and 38 C. Plants were harvested after 10 weeks.

Results. Although the cultivars differed from one another in growth habit, there was no detectable difference in growth habit associated with soil temperature treatment. Likewise, leaf bud cuttings taken from the two treatments did not respond differently in tuberization, although there were the expected differences among cultivars (Table B.7). As in past experiments in the hot greenhouse, Norchip and C1-884 had more tuberized cuttings than the other cultivars.

Fresh weights of haulms were not favored by cooling the soil. On the contrary, the average top growth was 23% higher from the hotter soils (Table B.8). Tuber growth was quite a different matter (Table B.9). The only cultivar to show even a trace of tuberization in the hot soils was C1-884. All of the cultivars tuberized at least slightly in the cooler soils, in spite of the very high air temperatures.

Fig.B.7. Total dry weights of plants from five cultivars grown in the phytotron in Israel under three temperature regimes, each at two photoperiods.

Fig. B.8. Percentage of dry matter partitioned to leaves in the experiment described in Fig. B.9.

Fig. B.9. Percentage of dry matter partitioned to stems in the experiment described in Fig. B.9.

Fig. B.10. Percentage of dry matter partitioned to tubers in the experiment described in Fig. B.9.

Discussion. It appeared from this experiment that the morphological response of the shoot to high temperatures and the attendant reduction in the degree to which the leaves were induced to tuberize were both unaffected by soil temperature. On the other hand, the expression of the induced condition, as reflected in tuber yield, did seem to be very responsive to cooler soil temperatures.

Table B.7. Degree of tuberization on cuttings taken from plants grown in the 40/30 C (day/night) greenhouse under two soil temperature regimes.

Cultivar	Tuberization Rating ^x		Mean
	Soil Temp. 23-27 C	Soil Temp. 30-38 C	
Norchip	3.7	3.8	3.8
C1-884	3.3	2.7	3.0
Katahdin	2.3	2.7	2.5
Desiree	2.3	2.6	2.5
LT-1	2.0	2.7	2.4
C14-343	2.1	1.6	1.9
Mean	2.6	2.7	

^x Two weeks after cuttings were taken, their buried buds were rated for degree of tuberization using a scale of 1 to 4: 4 = strongly induced to tuberize (sessile tubers); 1 = non-induced (no bud growth).

Table B.8. Fresh weights of haulms from plants grown in the 40/30 C (day/night) greenhouse under two soil temperature regimes.

Cultivar	Fresh weight of haulms (g/plant)		Mean
	Soil temp. 23-27 C	Soil temp. 30-38 C	
Norchip	386	504	445
C1-884	237	315	276
Katahdin	373	441	407
Desiree	340	437	388
LT-1	302	387	344
C14-343	285	275	280
Mean	320	393	

Table B.9. Tuber fresh and dry weights from plants grown in the 40/30 C (day/night) greenhouse under two soil temperature regimes.

Cultivar	Fresh wt., g/plant		Dry wt., g/plant	
	Soil temperature		Soil temperature	
	23-27 C	30-38 C	23-27 C	30-38 C
Norchip	122	0	17	0.0
C1-884	142	2	19	0.2
Katahdin	18	0	2	0.0
Desiree	50	0	6	0.0
LT-1	5	0	<1	0.0
C14-343	57	0	7	0.0

Experiment b.

To test these conclusions further, a second experiment was carried out in growth chambers. This time both air temperatures and soil temperatures were varied in a 2 X 2 factorial arrangement.

Materials and Methods. For each of the four treatments there were five replications of two cultivars, C1-884 and Katahdin. Plants were grown in growth chambers with 12-hour days and were watered daily. Each replication consisted of single plants grown from tubers in 14-cm plastic pots. Soil cooling or heating was achieved by circulating temperature-controlled water through copper coils that had been placed in each pot before planting the tubers. Treatments began 3 weeks after sowing the tubers and lasted for 7 weeks, at which time plants were harvested as in the earlier experiment. Soil and air temperatures were monitored by a CR21 data logger (Table B.10).

Table B.10. Mean soil and air temperatures measured in the growth chamber experiment.

Air	Soil	Day temperature, C		Night temperature, C	
		Air	Soil	Air	Soil
Cool	Cool	19	20	17	18
	Hot	19	32	17	31
Hot	Cool	34	19	30	17
	Hot	34	32	30	27

The results for both clones support the conclusions from the previous experiment that soil temperature has little effect on plant top growth (Table B.11) or on induction of leaves to tuberize (Table B.12). Induction ratings of cuttings taken from plants in the cool air were as high whether the soil was hot or cool. Similarly, the ratings for cuttings from plants

in the hot air were consistently low whether or not the soil was cooled (Table B.12).

Table B.11. Effects of air and soil temperatures on shoot and tuber dry weights of two clones. (Dry weights of aerial tubers are excluded.)

Treatment		Dry weights, g per plant			
		C1-884		Katahdin	
		Shoot	Tuber	Shoot	Tuber
Cool	Cool	13.3	23.8	12.8	26.0
	Hot	13.4	2.4	11.0	2.0
Hot	Cool	13.2	8.3	10.4	0.7
	Hot	13.3	1.9	14.4	0.0

Table B.12. Effects of air and soil temperatures on tuberization of leaf-bud cuttings from two clones.

Treatment		Induction ratings ^X		Ratio, tuber: leaf ^Y	
		C1-884	Katahdin	C1-884	Katahdin
Cool	Cool	9.0	9.0	0.5	0.4
	Hot	9.0	9.0	0.6	0.4
Hot	Cool	3.1	3.6	0.2	0.1
	Hot	3.1	3.7	0.0	0.1

^X Degree of tuber induction is rated subjectively on a scale of 1 to 9, where 9 = sessile tubers and 1 = no induction.

^Y Ratio of dry weight of tuber to dry weight of leaf of cutting.

There was an interesting response not shown in the data tables. In the treatment with cool air and hot soil, and only in this treatment, stolons grew up out of the soil and then formed green, aerial tubers.

Discussion. It would seem that the potential induction of the leaves to tuberize is affected principally by air, rather than by soil, temperature. On the other hand, the signal to tuberize is expressed most easily underground; and this expression is affected by soil temperature. When leaves were strongly induced by cool air temperatures, but expression of the induction was blocked by high soil temperatures, stolons grew vertically and tuberized only when they reached cooler temperatures, even though this was above the soil level. There is evidence in the literature that high air temperatures stimulate the production of gibberellins in shoot buds. It would be interesting to know whether high soil temperatures have a similar effect on the buds of stolons.

Experiment c.

An alternative to the explanation that high soil temperatures act directly upon underground buds in inhibiting the expression of tuberization is that roots grown in hot soils produce the inhibitor. This was tested by taking leaf-bud cuttings from induced plants, and burying the buds in hot vs. cool soils. Under these conditions, roots do not develop on the cuttings. Therefore any inhibition of the expression of tuberization would have to be directly via the effects on the underground buds.

Materials and Methods. Cuttings from induced plants of Norchip and Katahdin were taken, and the axillary buds buried in soil at either 25/20 C or 30/28 C day/night temperatures. Soil temperature was controlled as in the earlier experiments. Cuttings were kept in a mist bench under continuous light, all at the same air temperature. After 14 days they were rated for degree of tuberization on a scale of 1 to 9, where 1 = no growth of the buried bud, 9 = a sessile tuber at the buried bud, and intermediate values represent intermediate levels of induction.

Results. The temperature of the soil in which the axillary buds of cuttings were inserted had a marked effect on the degree of tuberization (Table B.13). In cool soils, all Norchip cuttings gave sessile tubers, demonstrating a very high level of induction to tuberize. As expected, the later maturing Katahdin was less induced than Norchip in the cool soil. In the heated soil, neither cultivar tuberized. The effect of soil temperature was very highly significant, and the interaction was significant at $p = 0.01$.

Table B.13. Effect of soil temperature in which axillary buds were buried on mean tuberization ratings for cuttings from two cultivars.

Soil Temperature Treatment	Cultivar	
	Norchip	Katahdin
Cool	9.0	6.0
Hot	2.3	2.7

Discussion. Clearly, even in the absence of roots, high soil temperatures inhibit tuber development. At least in this case the effects must be directly on the underground buds.

C. Possible Associations between Growth and Maintenance Respiration and Heat Tolerance (Cornell)

Wilson and Jones (1982) reported that selecting for lower rates of respiration gave higher yielding lines of *Lolium perenne*. Ecologists have reported that ecotypes adapted to more northern latitudes have a higher respiration rate and higher respiratory sensitivity to temperature than plants from more southerly latitudes (Lechowicz and Hellens, 1980). Conversely, plants adapted to desert climes have a lower respiration and

lower respiratory sensitivity to temperature (Pearcy, 1977) than plants adapted to cooler areas. Therefore, there is a logical basis for investigating the role of respiration in heat tolerance of potato.

Respiration is not to be viewed as a strictly negative process--low respiration rates may indicate a higher efficiency or simply an inactive plant. It is therefore useful to distinguish between substrate expenditure for growth and substrate expenditure which "maintains" the existing structures (Amthor, 1984, 1986). The distinction between growth and maintenance respiration is not based on any biochemical or compartmental distinction but is a functional distinction useful for whole plant physiologists (Amthor, 1984), especially for application in simulation models.

It is thought that maintenance respiration increases with rising temperature in a geometric manner (McCree, 1974; Amthor, 1984), while the efficiency of growth respiration is unaffected by temperature since it depends only on tissue composition.

There are several ways to determine experimentally coefficients for growth and maintenance respiration, two of which were adopted here. One commonly used technique utilizes a regression of respiration on growth over a period of weeks as a young plant progresses through rapid to slower growth (Szaniawski and Kieldiewicz, 1982). This gives M as the extrapolated point of zero growth and the slope as the growth coefficient, GR, where Y_G is the growth yield:

$$G_R = \frac{1 - Y_G}{Y_G}$$

The first experiment was an attempt to adapt this method by substituting differences in growth of individual leaves for differences among plants in a community.

The second and third experiments employed the dark starvation method, wherein plants are held in the dark for 30-40 h until respiration becomes stable (Amthor, 1984).

These and other methods used in determining respiration coefficients are subject to criticism (Amthor, 1984), mainly because any factor that affects growth also affects the maintenance component. However, the dark starvation technique has been used frequently and is relatively well accepted (Irving and Silsby, 1987). While the first method has not been used previously for individual leaves, the potential benefits seemed great. It would allow great savings of space and time, as well as direct comparisons between cultivars. The same growth chamber could be used for different cultivars concurrently, rather than requiring a separate chamber for each cultivar as in the original Szaniawski method.

Materials and Methods. The plants used in experiments 1 and 3 were from the standard set of six cultivars selected for these studies: C1-884, C14-343, Desiree, Katahdin, LT-1, and Norchip. In experiment 2 the Neo-tuberosum clone, A140-11, and two Andigena cultivars, Monserrate and Tomasa

Condemayta, were added to the original six. For experiments 1 and 2, plantlets from disease-free in vitro stem cuttings were set out in 13-cm clay pots in Cornell Mix in the greenhouse. In experiment 3, sprouts detached from mother tubers were the original plant material. In all three experiments the greenhouse temperature was set at 21 C day and 16 C night with supplemental 1000 W metal halide lights on 16-h per day. Plants were fertilized weekly with 15-7-14 Peters 'Peatlite Special' fertilizer solution.

Upon reaching the 6 to 10 leaf stage plants were grouped according to size into blocks which contained one plant of each cultivar. They were randomized and placed into a Sherer Model 37H growth chamber at the appropriate day/night temperature (28/26 for the 27 C measurement, 23/21 for the 22 C measurement, and 18/16 for the 17 C measurement). Plants were watered daily or as necessary and fertilized weekly with Peters 'PeatLite Special' (15-7-14). At no time was water stress allowed to develop. Photoperiods were 12 h, but the night cycle was reversed so that the lights were on from 8 pm until 8 am. Photon flux density (400 to 700 nm) in the chambers was 330-360 $\mu\text{moles m}^{-2} \text{s}^{-1}$ for experiment 1, and 360-400 $\mu\text{moles m}^{-2} \text{s}^{-1}$ for experiments 2 and 3. Plants were allowed to equilibrate for at least 10 days before measurements were begun. Care was taken to see that plants did not shade each other and that all leaves used had full illumination.

To estimate dry weight and relative growth rate in experiment 1, leaf dimensions (overall length, length and width of terminal leaflet, and length of the first two lateral leaflets) were measured two days prior to, and immediately subsequent to, determination of respiration. After the last measurements of leaf dimensions, actual leaf dry weights were taken. From these last two sets of data, multiple linear regression on a log-log scale was used to derive the equation and set of predictors (measurements of leaf dimensions) for each cultivar*temperature combination which, with the lowest variance, best predicted the dry weight of each leaf. The prediction equations typically had an $r^2 > 0.99$. Leaf relative growth rate (hereafter termed "relative growth rate") was estimated in the following manner:

$$\text{RGR (g g}^{-1} \text{ d}^{-1}) = \frac{\ln (\text{DW } 0) - \ln (\text{DW } -1)}{t},$$

where (DW 0) was the dry weight predicted by the regression model for the leaf dimensions at the time of harvest, (DW -1) was the dry weight predicted by the earlier measurements for the previous day, and t was time (d).

For experiment 1, plants were removed from the growth chamber at 8 am on the day of respiration measurement, double laminate polyethylene/nylon bags with inlet and outlet tubes connected were sealed around each of three leaves, and plants were placed in a cabinet at the appropriate temperature. Dimensions of the selected leaves had been previously measured. Ninety minutes or more were allowed for equilibration before measuring respiration at the midpoint of the dark cycle. Cabinet temperature, as well as temperature within each bag, was within 1 C of the setting. Airflow into the bags was controlled by a system of calibrated microcapillary tubes with water columns to maintain constant pressure. Duplicate samples were taken

from the outlet of each leaf chamber with a 5-ml plastic syringe and injected into the air inlet for the sample cell of a Grubb-Parsons model SB2 IRGA against a carrier gas of N_2 (method adapted from Clegg et al., 1978). Calibration was done with standard gas mixtures at three CO_2 concentrations. The IRGA response was linear in the range used. Immediately after the last respiration measurement the leaves were excised, the dimensions were again measured, and the leaves were dried at 70 C. Since it was difficult to achieve a good seal around the petioles of the upper two leaves to be measured without damaging them, they were cut off and enclosed in the plastic bag with air inlet and outlet attached. After 45 min equilibration in the dark at the specified temperature, respiration was measured as described above. Previous measurements showed that respiration did not differ significantly from that expected for attached leaves for 60 minutes following detachment (see Results).

In experiments 2 and 3, plants were held in the dark for 33-36 h; and the respiration of the attached leaves at the 6th, 7th, and 8th nodes from the top was measured as described above. These values were averaged for each plant.

To test the effects of shade on leaf respiration, one leaf of a pair of mature leaves on a plant was randomly selected and enclosed in a paper bag for one light period. The other leaf was left exposed to full illumination. Five pairs were used. Respiration was measured in the subsequent dark period.

To test the effects of detachment on leaf respiration, leaf respiration of 19 leaves was measured at about hour 8 of the dark cycle. The leaves were subsequently detached and respiration measured again 1 h later.

To test the assumption of the shape of the curve for the decline of respiration during the course of the dark period, the respiration of four attached leaves of one cultivar was monitored for a period of 30 h, beginning 1 h into the normal dark period.

Results. The effect of shading a single leaf for 12 h was to reduce respiration of that leaf by 41% (Table C.1).

Table C.1. Effect of shading on leaf respiration.

Pair	Light	Dark	Diff.
1	2.16	1.37	0.79
2	2.44	1.15	1.29
3	2.17	1.12	1.05
4	2.00	1.62	0.38
5	2.90	1.61	1.29
Ave.	2.33	1.37	0.96
sd.	.354	.240	.384

One h after detaching leaves, their respiration had declined by 0.12 mg CO₂ g⁻¹ h⁻¹ (n = 19), a 2.5% decline. Although this was slightly less decline than expected for attached leaves (Fig. C.1), it was well within the limits of accuracy of these experiments.

The data from the time course experiment fit reasonably well with a linear decline during the dark period (Fig. C.1).

Maintenance and growth respiration coefficients were calculated from the data in experiment 1 (Table C.2). The regression lines for each combination of temperature and cultivar gave average r^2 values of 0.643, 0.808, and 0.729, respectively, for 17 C, 22 C, and 27 C. (See Fig. C.2 and C.3 for a typical example.) Equality of means and then equality of slopes was tested in a combined analysis of variance with all data sets. The means for the treatment factors temperature and cultivar and the temperature X cultivar interaction for the slope were significantly different ($p < 0.001$).

Experiment 1 seemed to show that the change in maintenance requirement with increasing temperature is quite different with different cultivars (Table C.2). Katahdin increased from 0.034 to 0.051, a 50% increase, while other cultivars increased only slightly, or in the case of Norchip, even decreased between 17 C and 27 C. Nearly all cultivars were higher at 22 C than 17 C. The main reason that the maintenance coefficient (M, the intercept of the regression line) did not increase in a similar manner for all cultivars was the change in the growth coefficient (G, the slope of the regression line). At higher temperatures G was higher for some cultivars, which resulted in a lower estimate of M, since the intercept of the regression line depended partly on the slope.

The main cause of the interaction was that the cultivars C1-884, Desiree, LT-1, and Norchip had increasing slope, while the cultivars C14-343 and Katahdin had constant or decreasing slope, with increasing temperature (Table C.2). At 17 C the four cultivars had lower growth respiration coefficients than C14-343 and Katahdin, while at 27 C the relationship was reversed (Table C.2). Figures C.4 and C.5 show this trend for four of the six cultivars.

Table C.2. Growth and Maintenance Respiration Coefficients. The intercept and slope were calculated as shown in Fig. C.2. Each pair of values represents measurements of 30-40 leaves.

Cultivar	Temperature					
	17 C		22 C		27 C	
	M	G	M	G	M	G
C1-884	.046	.190	.049	.239	.045	.322
C14-343	.039	.262	.046	.270	.044	.259
Desiree	.037	.204	.051	.197	.039	.301
Katahdin	.034	.278	.045	.247	.051	.241
LT-1	.038	.224	.028	.327	.041	.287
Norchip	.044	.197	.048	.225	.039	.344

TIME-COURSE
C1-884
22 C

Figure C.1. Time-course experiment. Position designates the leaf position from the top. Time is from the beginning of the normal dark period.

C1-884
17 C
combined data set

Figure C.2. Method 1 for calculating regression lines. Each point represents one leaf. Same data set as in Figures 3 and 4.

C1-884
17 C
AVERAGED FOR LEAF POSITION

Figure C.3. Method 3 for calculating regression:
lines. Each point is the average value for a
leaf position. Same data as in Figures 2 and 3.

Growth and maintenance respiration
regression lines
17 C

Figure C.4. A comparison of four varieties at 17 C.

Growth and maintenance respiration
regression lines
27 C

Figure C.5. A comparison of four varieties
at 27 C.

Experiments 2 and 3 showed differences between cultivars in the level of maintenance respiration as determined by the dark-starvation method (Tables C.3 and C.4, respectively). Cultivar C1-884 consistently had the lowest respiration of the cultivars tested (main effect of C1-884 different from all other cultivars in experiment 3, $p < 0.05$).

Table C.3. Respiration at 22 C after dark starvation, Experiment 2. Each value represents the mean of seven plants. The three youngest fully expanded leaves of each plant were averaged to give the value for a plant.

<u>Cultivar</u>	<u>Respiration</u> <u>mg CO₂ g⁻¹ h⁻¹</u>
C1-884	1.31 a
Katahdin	1.44 a
LT-1	1.60 ab
C14-343	1.62 ab
Norchip	1.66 ab
Tomasa C.	1.72 ab
Monserate	1.89 b
Desiree	1.90 b
A140-11	1.97 b

Table C.4. Respiration (mg CO₂ g⁻¹ h⁻¹) after dark starvation, experiment 3. Each value represents the mean of six plants. Different letters within a column indicate values are significantly different at the $p = 0.05$ level by Duncan's multiple range test, except for averages for each temperature, where comparisons are within the row.

<u>Cultivar</u>	<u>Temperature, C</u>			<u>AVG</u>
	<u>17</u>	<u>22</u>	<u>27</u>	
C1-884	1.11 a	1.25 a	1.48 a	1.29 a
C14-343	1.39 a	1.56 bc	1.69 a	1.56 b
Desiree	-	-	2.25 c	-
Katahdin	1.29 a	1.43 abc	1.75 a	1.50 b
LT-1	1.11 a	1.66 c	1.81 ab	1.55 b
Norchip	1.34 a	1.32 ab	2.15 bc	1.62 b
AVG	1.25 x	1.44 y	1.78 z	

Discussion. The new technique used in experiment 1 allowed a large number of samples (180) to be completed in one week. This represented 30 leaves each of six clones, enough to make conclusions about the growth and maintenance coefficients for the six clones at one temperature. In this sense the technique seemed promising as a possible tool to use in making final selections of parents in a breeding program, but not as a selection criterion for progeny. If only respiration were measured, the set-up could be modified to further increase the number of daily measurements.

The results show that in making measurements of respiration, care must be taken to only use leaves which are not significantly shaded by other leaves. The leaf detachment experiment confirmed that the method of detaching the smaller leaves before making respiration measurements was reasonable, provided respiration was measured within 1 h of detachment. The time course experiment showed that the midpoint of the dark period was an appropriate time to measure respiration as an estimate of average respiration for the 12-h dark period.

However, the respiration patterns observed in experiment 1 were anomalous. That the maintenance requirement did not double as would be predicted by a Q_{10} of 2 is not surprising, since at higher temperatures growth rates were somewhat lower (Part E2) and would be expected to result in a lower maintenance respiration requirement. However, one would not expect the maintenance respiration rate to decline with increasing temperature, while the growth coefficient, assumed to be unaffected by temperature (Lambers et al., 1983), increased. One of the most obvious explanations for a changed growth coefficient would be a change in the tissue composition at the higher temperatures; yet to achieve the observed 84% increase in growth coefficient (cultivar Norchip) would require an unrealistically high increase of protein, lignin, or lipids.

Another possible explanation, increased activity of the alternate oxidase system, is not supported by the data. A decreased efficiency of respiration ought to be reflected both in higher growth respiration coefficients and in higher maintenance respiration coefficients, which was not the case here (Table C.2).

The more likely possibility for the anomalous patterns is that the altered respiration characteristics reflect a change in the partitioning patterns within the shoot. Developing leaves are not fully autotrophic, but obtain part of their necessary substrates for growth from other leaves. This means that normally part of the respiration of older leaves is actually growth respiration for the benefit of younger leaves. Reducing the amount of growth respiration donated by older leaves to developing leaves would increase the observed "growth respiration" requirement of the younger ones and cause a lower observed "maintenance coefficient" as a result of the higher slope used in its estimation. This is a serious shortcoming of the method used here, which negates the usefulness of the derived growth and maintenance coefficients.

Nevertheless, the cultivar X temperature interaction for the growth coefficient does indicate that the method provides some physiologically useful information. The same cultivars whose growth coefficients were least affected between 17 and 27 C, C14-343 and Katahdin, also had higher rates of

leaf production and relative growth rates at 27 C (Part E2). This would be the case if within-shoot partitioning was unaffected by temperature while growth rates increased with higher temperature. The increased growth coefficients and constant or reduced leaf production and growth rates of the other four cultivars between 17 and 27 C would be consistent with a decreased supply of assimilate from lower leaves and greater autonomy of the younger leaves.

It would seem that this method might still be applicable if an organ with a uniform carbon source were used. For potato, likely plant material might be young growing tubers or potato sprouts attached to mother tubers.

The dark starvation method appears to be quite consistent, since the values determined for four of the five cultivars common to both experiments were within 5% at the same temperature; and C1-884 had the lowest value in both experiments (Tables C.3 and C.4). However, it is difficult to interpret what the meaning of the differing levels of dark-starved respiration might be. The heat-sensitive cultivar, Katahdin, was intermediate at all temperatures, as well as for respiration increase with increasing temperature. The early, heat-tolerant cultivars C1-884 and Norchip, which had similar responses in experiment 1, were dissimilar for both respiration rates and increase with higher temperatures. Likewise, there was no clear trend with origin of plant material. In experiment 2, both the Tuberosum and Neo-tuberosum types had cultivars with low, middle, and high rates of dark-starved respiration.

The cultivar C1-884 has the highest harvest index of any of the clones used (Part A) and may be exceptionally rapid in exporting current photosynthate, so that respiration after 30 h is lower than for other cultivars. Although respiration is proportional to the level of available assimilate, it is assumed that maintenance respiration is independent of assimilate levels (Amthor, 1984). These experiments may cast doubt on this assumption. Therefore, it seems likely that the dark-starvation method of estimating maintenance respiration is also subject to the complication of within-shoot partitioning and translocation rates.

In experiment 3 the level of maintenance respiration rose only 42% with a 10 C increase in temperature (Table C.4). In an earlier experiment the value was 44% (not shown). Although the values for single cultivars varied from 22%-63%, a test for homogeneity of slope showed no significance for different slopes at the 5% level ($p = 0.118$). The rise in maintenance respiration with temperature reported here is much lower than the estimates in previous reports (McCree, 1974; Szaniawski and Kielkiewicz, 1982). This may be due to the longer equilibration time growing at the experimental temperature. Alternatively, there may be some factor in potato which allows a greater proportion of usable assimilate to be exported, so that there is less assimilate available after a period of 33-36 h in the dark at the higher temperature.

Conclusions. The method in experiment 1 proved inadequate for giving reliable estimates of the growth and maintenance respiration coefficients to answer the questions: are there genotypic differences in the maintenance and growth respiration components between potato cultivars and, if so, are those differences partly responsible for "heat tolerance?" The results did,

however, indicate that there are cultivar differences in temperature response for some physiological components which are reflected in altered estimates of the growth respiration coefficients and which are probably related to partitioning within the shoot. Experiments 2 and 3 demonstrated that the dark starvation method may be used to show differences between cultivars, but the relationship to yield and temperature performance is not known.

As more is learned about the different aspects of heat tolerance in these cultivars it may become possible to determine whether the observed differences in respiration are correlated with their respective yield performances under warm conditions.

D. Heat Tolerance and Photosynthesis

1. Experiments with S. tuberosum (Israel)

Materials and Methods. The effect of heat stress on photosynthesis of six potato varieties was examined in Israel during the years 1985-1986. Plants were grown in the soil in two greenhouses. Temperature regimes (day/night) were 31-33/19-21 C and 38-42/19-21 C, respectively.

The effects of day temperature and daylength on single leaf photosynthesis were studied in the phytotron. Plants of Alpha and Desiree were grown, using seed tubers, in 20-cm black pots at 22/12 and 32/12 C (day/night) temperature regimes. Vapor pressure deficit was the same under the two temperature regimes. Daylengths were 8 h and 16 h. The short day treatment was obtained by transferring the pots to a dark room, and the long day plants were left under natural light for approximately 10-11 h; the other 6 h were completed with dim lights. All the measurements were taken under natural light between 10-12 AM, after the plants were irrigated. Photosynthesis rates of both varieties were similar throughout the season; therefore, results are expressed as means of both varieties.

Single leaf photosynthesis was measured with a portable photosynthesis system (Li-Cor LI-6000) through the growing season in both the greenhouse and the phytotron experiments. Leaf senescence was examined by tagging leaves of three varieties (Desiree, Up-to-Date, and C1-884), when they reached lengths of 3.5 cm and taking photosynthesis measurements throughout the season.

Photosynthesis rate of aging leaves was measured repeatedly during the season in three leaves which appeared at different stages. The gas exchange measurements were taken after exposing the leaf to direct sunlight, out of the canopy.

To determine the effects of acute heat stress (heat shock), uptake of CO₂ (net photosynthesis) and water-vapor exchange were determined in an open gas-exchange system. An attached terminal leaflet was placed in a perspex

chamber such that 7 cm² of leaflet area was exposed to light and gas flow. The relative humidity was kept at 80% by bubbling the air, prior to its entering the chamber. Light was provided by a 400-W mercury lamp and irradiance level was regulated by layers of miracloth. Light was passed through a 5-cm water filter before reaching the leaf chamber.

Results.

1) Prolonged heat stress

Only small differences or no differences at all were observed between leaf photosynthesis in the two greenhouses in either 1985 or 1986. No significant differences were observed among the cultivars (Figs. D.1, D.2, D.3, D.4, D.5, D.6). Values of leaf photosynthesis under heat stress (above 40 C) were up to 30 micromoles of CO₂ per m² of leaf area per second. These plants were grown under the heat stress from emergence.

Likewise in the phytotron no significant differences in the photosynthesis of the first fully expanded leaf were observed between the two temperature regimes at any plant age, although rates decreased with age in both regimes (Fig. D.7). Ambient temperature during photosynthesis measurement was actually 2-4 C above the planned regimes so, in fact, temperatures of 34-36 C did not cause a reduction in photosynthesis compared to 24-26 C.

Values of leaf resistance and transpiration are parameters that may indicate whether photosynthesis is limited due to stomatal closure. High temperatures (40 C) caused a reduction in leaf resistance of the three varieties. As a result, leaf transpiration was increased, indicating that no water stress accompanied the extreme heat stress. High temperatures had a significant effect on stomatal resistance (Fig. D.8). As compared to the control, stomatal resistance of leaves grown under high temperature regimes in the phytotron was low throughout the season.

Calculation of the ratio between photosynthesis rate (P) and sub-stomatal CO₂ concentration (C_i) is a measure of the mesophyll activity efficiency. In the phytotron this ratio was lower with 32 C days than with 22 C days (Fig. D.9). In the greenhouse experiment heat stress caused a significant reduction in P/C_i ratio of Desiree and Up-to-Date but not in Cl-884 (Fig. D.10).

High temperature conditions were accompanied by a higher compensation point for CO₂ of the three varieties (Fig. D.11).

2) Leaf age

Maximum values of photosynthesis in the 1986 greenhouse experiment were obtained when leaves were young (3.5 cm), declining through leaf development and senescence (Figs. D.12). CO₂ exchange rate values of young Up-to-Date leaves under heat stress appeared smaller than Desiree and Cl-884 (Figs. D.12). A sharp decline in photosynthesis with leaf ageing was observed along the season in the phytotron. This was more pronounced under the high temperature regime (Fig. D.13).

Fig. D.1. Rates of net photosynthesis of leaves of six cultivars grown in the cooler greenhouse (33/21 C) in Israel, measured at four intervals after planting, 1985.

Fig. D.2. Same as Fig. D.1, but data for the hot (41/21 C) greenhouse.

a. Full expanded leaf - C1-884.

b. Full expanded leaf - Désirée.

Fig. D.4. Leaf photosynthesis, Greenhouse, 1986.

70

a. Full expanded leaf - Norchip

b. Full expanded leaf - Up-to-Date.

Fig. D.5. Leaf photosynthesis, Greenhouse, 1986.

a. Full expanded leaf - C14-343.

b. Full expanded leaf - LT-1.

Fig. D.6. Leaf photosynthesis, Greenhouse, 1986.

a. Full expanded leaf - control.

b. Full expanded leaf - hot treatment.

Fig. D.7. Phytotron experiment. Mean values for Alpha and Désirée.

Fig. D.8. Phytotron experiment. Mean values for Alpha and Désirée.

Fig. D.9. Phytotron experiment. Mean values for Alpha and Désirée, three leaf ages.

Fig. D.10. Greenhouse, 1986. Values are means for 0 and 6 days after leaf appearance.

Fig. D.11. Greenhouse, 1986.

Fig. D.12. Leaf senescence, greenhouse experiment, 1986.

Fig. D.13. Phytotron experiment.

3) Heat shock (acute heat stress)

In the heat shock experiment, photosynthesis rates were affected by growing conditions. Acute exposure of a single leaf to high temperature conditions was accompanied by a significant reduction in CO₂ fixation (Fig. D.14). A clear reduction in photosynthesis rates was observed at 35 C, as compared to 25 and 15 C (data not shown). The marked effect of temperatures in this experiment appear to be a result of the acute exposure of the leaves to high temperature conditions. However, when plants were moved back to moderate temperatures, a significant increase in photosynthesis rates was observed (Fig. D.15).

4) Night temperature

Acute exposures to different temperature regimes affected photosynthesis, but CO₂ fixation was also affected by the plant's previous growing conditions. When plants were grown under different night temperatures, net photosynthesis rates were higher for those which were grown at 12 C night temperature than at 22 and 27 C (Fig. D.16).

5) Daylength

The photosynthesis rate of the first fully expanded leaf was affected by daylength: rates of leaves that were grown under long days were higher than under short day conditions. The differences were greater at the end of the season than at the beginning (Fig. D.17). The different photosynthesis rates are assumed to be a result of differences in mesophyll activities, as indicated by the P/Ci ratio (Fig. D.18). A possible reason for those differences was the high total chlorophyll (a+b) concentration observed in leaves grown under long days (Fig. D.19).

Discussion. Previous workers have found a sharp decline in photosynthesis rates at temperatures higher than 30 C. Except for the heat shock experiment, decreases were much less severe in the present study. The apparent discrepancy is due to differences in experimental methods. Most of the response curves of photosynthesis to temperature which are cited in the literature have been for leaves that were measured after fairly short adaptation periods to the treatment temperature. The CO₂ fixation rate values expressed in Fig. D.7 and Figs. D.1, D.2, D.3, D.4, D.5, D.6 indicate a relatively high adaptive capability of the photosynthetic system of the potato plant to high temperature.

Rates of carbon dioxide fixation declined as leaves aged, with the decline slightly more rapid at high temperatures. Rates were affected by photoperiod more than by temperature as leaves aged. The higher photosynthetic rates under longer days were associated with a higher chlorophyll content. The fact that long days delay maturity may be a contributing factor, which would be consistent with the fact that the late maturing cultivar Up-to-Date showed less decline with age (Fig. D.12). Growing plants at high night temperatures decreased daytime rates of photosynthesis.

Differences among cultivars in response to daytime temperatures did not appear to explain differences in heat tolerance. For all cultivars, there

Fig. D.14. Heat shock experiment, Désirée. Photosynthesis rate after 48h of heat stress, compared to control.

Fig. D.15. Heat shock experiment, Désirée. 1 = heat stress for 24 h at 32/27°C; 2 = recovery for 24 h at 27/22°C; 3 = continuous 27/22°C.

Fig. D.16. Effect of night temperatures during growth on net photosynthesis of Désirée.

Fig. D.17. Phytotron experiment. Mean values for Alpha and Désirée.

Fig. D.18. Phytotron experiment. Mean values for Alpha and Désirée.

Fig. D.19. Phytotron experiment.

tended to be a decrease in carbon dioxide fixation with increasing temperature at which plants were grown. There was evidence that this was a result of increasing mesophyll rather than stomatal resistance. In the phytotron, stomatal resistance actually decreased at high temperatures, whereas there was little or no effect on photosynthesis. Also, there was a difference in the P/Ci curves (Fig. D.9) in both the phytotron and greenhouse experiments, indicating increased mesophyll resistance.

The low stomatal resistance under high temperature conditions could be of benefit to the plant photosynthetic system in two ways:

- a) Cooling the leaves by a rapid latent heat emission from the leaves to the air, due to higher transpiration rates (Fig. D.20).
- b. Increasing photosynthetic activity as a result of a higher CO₂ concentration in the sub-stomatal cavities, due to wider stomatal aperture under high temperature (Fig. D.21).

2. Maximal rates of O₂ evolution in wild Solanum species (Cornell)

In work supported by other funds we had screened a large number of Solanum species for heat tolerance, as reflected in shoot growth at high temperatures. (In these experiments photoperiods were maintained at 18 h, completely inhibiting tuberization.) Degree of heat tolerance had been assessed by comparing growth of accessions in a hot and in an ambient temperature greenhouse. (The greenhouses are described in Part A2, Experiment 1). Because rather substantial differences were found among accessions within some of the species, we decided to examine the relationship between heat tolerance and O₂ evolution during photosynthesis as part of our studies on the physiology of heat tolerance. This was a deviation from the overall plan, which was to work with a standard set of S. tuberosum cultivars; but the differences in reaction to heat stress were so striking in some of the wild species that it seemed worthwhile to make an exception, especially since the plants were already available to us because of the work on the other project.

Materials and Methods. Rates of O₂ evolution from leaf discs (normalized to chlorophyll content) were measured at 40 C under optimal CO₂ and light, using plants that had been acclimated to 40 C for 1 to 3 days. For comparison plants of S. chacoense were grown and measured at 23 C, with no acclimation to 40 C. For each leaf node, data for the maximum rates of O₂ evolution are presented as the ratio of the rate of the sensitive to that of the tolerant accession. Ratios less than one indicate that the tolerant accession exceeded the sensitive accession in maximum rate of photosynthetic O₂ evolution.

Results and Discussion. For all four species examined, the average maximum rate of O₂ evolution at 40 C was higher for heat tolerant than for sensitive accessions (Table D.1). In general the difference between sensitive and tolerant accessions increased with increasing leaf age, as evidenced by decreasing ratios (Table D.1). The regression of ratio on node number was significant at $p = 0.01$. In contrast, at 23 C the sensitive accession gave maximum rates at least as high as in the tolerant accession, and ratios did not decline with increasing leaf age (Table D.1).

Fig. D.20. Phytotron experiment.

Fig. D.21. Phytotron experiment.

These data suggest that in the four species examined sensitivity to chronic heat stress, as reflected in reduced shoot growth, is associated with reduced efficiency of the light reactions of photosynthesis. The relationship is most apparent in older leaves.

Table D.1. Mean ratios of maximum rates of O₂ evolution for heat sensitive and heat tolerant accessions of four Solanum species at 40 C, measured at different leaf ages.

Temp.	Species	Leaf age (node number)									
		3	4	5	6	7	8	9	10	11	12
40 C	<u>S. stoloniferum</u>	1.05	1.12	nd	.96	.81	.86	nd	.78	nd	.65
"	<u>S. bulbocastanum</u>	nd ¹	.90	1.30	.75	.84	1.09	nd	.89	nd	.89
"	<u>S. demissum</u>	nd	nd	.95	.78	.85	.85	.93	.65	nd	nd
"	<u>S. chacoense</u>	nd	.80	.95	.45	.43	.50	.67	.44	nd	nd
	Mean, 40 C	1.05	.94	1.07	.73	.73	.82	.80	.69	nd	.78
23 C	<u>S. Chacoense</u>	1.10	1.25	nd	1.03	.88	nd	nd	1.10	1.26	nd

¹nd = no data

Regression equation: ratio = -0.04(node number) + 0.81

3. Fluorescence (Cornell)

Introduction. All photosynthetic tissue re-emits, in the form of chlorophyll fluorescence, a tiny fraction of the light it receives (Papageorgiou, 1975). Changes in photosynthetic metabolism are reflected as transients in fluorescence yield, and these can be detected and recorded without interfering with tissue integrity. Smillie et al. (1983) concluded that fluorescence measurements of wild and cultivated potato species could be used to distinguish heat and cold tolerant accessions, but measurements of fluorescence yield were taken only in response to acute temperature stress (10 min at 41 C, in the case of heat stress).

One component of heat tolerance may be enhanced thermostability of the photosynthetic apparatus. To determine if this is the case it is desirable to consider changes in photosynthetic metabolism occurring after chronic heat stress, as well as acute heat stress, inasmuch as acclimation to chronic stress occurs in many species.

Pairs of heat tolerant and sensitive accessions of several Solanum species (see previous experiment) were used for the experiment. The method

for detection of delayed fluorescence (Ellenson, 1986) was adapted for the measurement of tissues subjected to heat stress.

Materials and Methods. Delayed fluorescence from potato leaf tissue was measured at different temperatures by placing 1-cm leaf discs on moist paper, on top of a thermal plate, protected from desiccation with transparent plexiglass. A fiber optic placed at the plexiglass immediately above the sample allows saturating flashed light (frequency of 4 hz) to excite the sample. Between flashes the fiber optic transmits delayed fluorescence to a photomultiplier. The temperature is changed by altering the temperature of water which circulates inside the thermal plate.

Delayed fluorescence was measured at temperatures ranging from 20 C to 45 C, using leaf discs from plants grown at 35/30 C or 25/20 C, day/night temperatures. Photoperiods during plant growth were 18 h, ensuring that there was no tuberization to complicate the response of the shoots to the temperature regimes. In general measurements were made on pairs of heat sensitive and tolerant accessions from a given species. Both young and old leaves were sampled. Measurements generally started at a low leaf disc temperature, which was increased in steps and then decreased again. Intervals between readings were 6 min if there was no change in disc temperature; 10 min if temperatures were changed.

Results. Of five pairs examined, three showed little or no difference in delayed fluorescence and two showed a clear difference in favor of the more heat tolerant accession. Data for the latter two pairs are presented. Fig. D.22 shows data from two accessions of *S. bulbocastanum* that had been exposed to two days at 35/30 C after several weeks at 25/20 C. Leaf discs were from older leaves (eighth node from the apex). Delayed fluorescence was measured while disc temperatures were increased from 22 to 46 C, and then lowered back down to 22 C. The temperature for each measurement is indicated. Each data point represents the peak delayed fluorescence yield during a cycle of 100 flashes. At temperatures above 41 C, delayed fluorescence yield fell sharply for the heat sensitive accession, while the decrease was much more gradual for the tolerant accession.

Results from a similar experiment with *S. stoloniferum* are shown in Fig. D.23. In this example the plants had been subjected to heat stress for 10 days prior to measurements. The delayed fluorescence yield was equal for the two accessions at 25 C, but as the temperature increased the yield increased much more sharply for the resistant accession.

Discussion. Preliminary results such as the above examples suggest that delayed fluorescence measurements may be useful in demonstrating differences in the response of the photosynthetic apparatus between heat tolerant and sensitive genotypes. Similar results have been obtained with bean species, using the same experimental procedures. In both potato and bean it appeared that differences between tolerant and sensitive genotypes were more pronounced when older leaves were sampled. Lack of detectable differences in some pairs could be attributable to inadequacies in the methodology employed; alternatively, it may be that the basis for differences in tolerance in those particular pairs was not associated with photosynthesis.

Fig. D.22. Effect of temperature on maximum delayed light emission during induction on mature, heat acclimated leaf tissue of *S. bulbocastanum* accessions. Two accessions of *S. bulbocastanum*, one of which ($\triangle$ — $\triangle$) had exhibited a greater ability to produce dry matter in hot growing conditions than the other ($\times$ — $\times$), were tested. Both plants had been raised at 25/20 C, then acclimated at 35/30 C for 2 days prior to delayed light emission (DLE) measurements. DLE is measured in arbitrary units.

Fig. D.23. Effect of temperature on maximum delayed light emission during induction on mature, heat acclimated leaf tissue of *S. stoloniferum* accessions. Experimental conditions were the same as for Fig. D.22, except that heat acclimation was for 10 days, and heat tolerant (△—△) and sensitive (×—×) accessions of a different species were used.

As yet these data cannot be interpreted in specific metabolic terms. The ability to do so would greatly enhance the value of such a technique in screening for thermostability of the photosynthetic apparatus. As a step in this direction, an apparatus is being constructed that will measure simultaneously variable fluorescence and delayed fluorescence. Since variable inflorescence transients are better understood in specific metabolic terms (see review by Krause and Weiss, 1984), their simultaneous measurement should assist in interpreting delayed fluorescence transients. The advantage of measuring delayed fluorescence is that it is sensitive to metabolism on the oxidizing side of Photosystem II, i.e., the oxygen evolving complex; whereas variable fluorescence is sensitive only to metabolic events on the reducing side of Photosystem II.

E. Effects of Heat Stress on Developmental Patterns and Partitioning.

1. The effect of temperature and photoperiod on tuberization of potato cuttings (Growth chamber experiment, Cornell)

It is generally accepted that induction of potatoes to form tubers is favored by short days and cool temperatures. This is not to say that all varieties are induced at the same photoperiod, however. Rather, the potato will tuberize when the photoperiod is shorter than a particular daylength, and this critical photoperiod varies among cultivars and clones. Induction is also favored by cooler temperatures, typical of temperate zone summer nights, with the effects differing among cultivars. As demonstrated in the greenhouse experiments (Part A), heat stress reduces the amount of assimilate partitioned to tubers. The interactions between temperature and photoperiod on inducing cultivars to tuberize are not clearly understood. This set of experiments examines these interactions using six cultivars and clones, with two temperatures and two photoperiods.

Cuttings have been suggested as a tool to study heat tolerance in potatoes, since tuberization on cuttings reflects the degree to which a plant has been induced to tuberize (Ewing and Wareing, 1978). Warm temperatures give poor yields partly because tuber induction is poor (Ewing 1981, 1985). The ability of cuttings from plants with a long critical photoperiod to form tubers from the buried bud has been correlated with early tuberization in the full plant (Rasco et al., 1980). In the following experiments, cuttings were used to test whether or not plants were induced to tuberize under the treatment conditions.

Materials and Methods. Four growth chambers (Sherer Controlled Environment Chambers) were used in a 2 X 2 factorial experiment of temperature and photoperiod. The design was a randomized complete block - split plot, with temperature and photoperiod serving as the main plots and cultivars as the sub-plots. There were three replications, conducted over time. The temperatures used were 30 C day with 25 C night, and 20 C day with 15 C night; photoperiods were 10 h and 16 h. Photoperiod was extended in the long day treatments by using low level, non-photosynthetically active

incandescent light. Otherwise, the light treatments were achieved with the use of twelve 50-W incandescent and sixteen 15-W cool white fluorescent bulbs in each chamber. "Day" temperature, from 0800 to 1800 hours, was at the same time as full light. Photoperiod extension in the long day chambers was from 1800 to 2400 hours. Temperature and light switching was controlled automatically.

The cultivars used were Katahdin, Norchip, Desiree, LT-1, C1-884, and C14-343. For the first two replications, plantlets from test tubes were transplanted into 13-cm clay pots filled with Cornell Peat-Lite mix (Boodley and Sheldrake, 1973), and were grown in the greenhouse for approximately 2 1/2 weeks before being placed into growth chambers. For the latter two weeks of this period, they were grown under mercury halide lamps to insure adequate light to avoid etiolation. For the third replication, 15 to 20 g tubers were used rather than plantlets. After emergence, these were placed under the halide lamps. Plants were fertilized with nutrient solution, and sprayed with insecticides before being put into chambers. At all times prior to the onset of treatments in growth chambers, plants received 24-h lighting to avoid induction. About twice as many plants as would be needed for each replication were grown so that uniform plants could be selected for the experiment. Plants were pruned as needed to one main stem. These were staked to keep plants erect while in chambers. The schedule is shown in Table E.1.

Table E.1. Schedule of Growth Chamber Experiments.

<u>Replication</u>	<u>Transplant</u>	<u>Cuttings</u>	<u>Treatment</u>	<u>Rating</u>
I	2-9-84	3-22-84	2-28-84	4-4-84
II**	3-8-84	5-23-84	4-26-84	6-7-84
III	8-30-84	10-9-84	9-17-84	10-23-84
IV	7-13-85*	9-15-85	8-28-85	10-1-85

* planted tubers for this replication, rather than plantlets.

** this replication was discarded due to insect infestation in growth chamber. replications III and IV are renumbered II and III.

Three one-node cuttings were taken from each plant. These were taken from the fourth, fifth, and sixth nodes from the apex, with node number one being the youngest node which had a leaf at least 35 mm in length. Cuttings were inserted into Cornell Mix in polystyrene trays, with the bud buried and the leaf emerging above the surface. Trays with cuttings were put into mist benches, where light was continuously supplied with the use of 50 W incandescent bulbs to avoid further tuber induction.

At the end of two weeks in the mist bench, cuttings were evaluated for degree of induction by rating the type of growth from the buried bud, using

a scale of 0 to 4: 0 = no growth from the axillary bud; 1 = shoot growth from the axillary bud; 2 = ancillary tuber(s) formed at either side of the axillary bud; 3 = a tuber formed at the end of a stolon from the axillary bud; and 4 = a sessile tuber formed at the axillary bud. Higher numbers reflect increasing degrees of induction to tuberize.

In addition, tubers were severed from shoots, and dry weights of tubers and shoots were determined. Dry weights were expressed as: 1) the total dry weight of tubers produced by the 15 cuttings (five plants X three cuttings/plant), 2) the ratio of tuber to shoot dry weights, and 3) the percentage of the 15 cuttings that had sessile tubers.

Results and Discussion. The four methods of expressing the degree of induction to tuberize were significantly intercorrelated at $p = 0.01$. There was only one significant three-way interaction, which was on the dependent variable, tuber dry weight (Table E.2) with a p -value of 0.043. This interaction reflects the fact that cultivars responded differently to photoperiod depending on whether it was cool or hot. For example, Norchip had much higher tuber dry weight with the cool treatment than with the hot one under long days (Fig. E.1a); but with short days the response to temperature was negligible (Fig. E.1b). Contrarily, Katahdin had a much higher response to cool temperature under short days than did any other cultivar; but under long days there was little tuberization for Katahdin at either photoperiod (Figs. E.1a and E.1b). In general the response to the difference in photoperiods was greater than the response to the temperature treatments; but it is clear that both long days and high temperatures tended to reduce the level of induction to tuberize.

Table E.2. Summary of analysis of variance tables of the effects of temperature and photoperiod on the tuberization status of cuttings of potato.

	df	Tuber DW	Tuber/Shoot DW	Mean Rating	% Sessile Tubers
Temp	1	ns	ns	*	ns
Photo	1	**	**	***	***
T X P	1	ns	ns	ns	ns
Var	5	**	***	***	***
T X V	5	ns	ns	ns	ns
P X V	5	ns	ns	***	***
T X P X V	5	*	ns	ns	ns
C.V.		42.8	32.4	14.8	27.8

significance: * = 0.05 level, ** = 0.01 level, *** = 0.001 level, ns = not statistically significantly different at $p = 0.05$

Fig. E.1. The effects of photoperiod and temperature before cutting on tuber dry weight of cuttings taken from six cultivars.
a. Photoperiod = 16 h; b. Photoperiod = 10 h.

2. Rate of leaf production and decline of relative growth rate (Cornell)

The data obtained in the experiment to determine growth and maintenance respiration coefficients (Part C) were also analyzed for growth rate to verify the assumptions of growth in the Ng and Loomis (1984) simulation model and to check for differences among cultivars.

Materials and methods. Plants were grown as described in Part C. Leaf appearance rate was determined for the youngest three leaves of each plant during the data collection period. The relationship of temperature to relative growth rate and its decay with age was estimated by regressing relative growth rate against leaf position (from the top).

Results. The temperature X cultivar interaction for leaf appearance rate was significant at $p = 0.06$ (Fig. E.2). All cultivars increased in a similar manner from 17 to 22 C, but from 22 to 27 C, only C14-343 continued increasing at a similar rate, while Desiree, Katahdin, and Norchip increased slightly, and C1-884 even decreased its leaf production rate. LT-1 increased its rate at slower but even increments with increasing temperature.

In the analysis of variance for the mean relative growth rate, the temperature X cultivar interaction was significant at $p = 0.01$. The mean relative growth rate rose for all cultivars between 17 C and 22 C, but C14-343 and Katahdin were significantly different from C1-884 and Norchip at 27 C. For the mean and linear coefficients (Table E.3), LT-1 was the cultivar least affected by temperature. The early cultivars C1-884 and Norchip were notable in having a lower mean as well as a slower rate of decline (linear coefficient) than the other cultivars at 27 C, but Norchip had a high mean and slope at 17 and 22 C.

There were insufficient small leaves for good estimates of maximum relative growth rate, or growth in the logarithmic phase. Although plots of the entire data set had a sigmoidal shape (not shown) indicating that this maximum was being approached, there were too few points in this range to estimate the maximum for most individual temperature X cultivar combinations. For this reason a quadratic polynomial model describing the lower part of the curve was employed, rather than the non-linear function which would have described the entire curve had there been sufficient points. The analysis of variance did not show significant differences for unique quadratic terms; therefore the model used the averaged quadratic, which had a value of 0.00316. Since it is difficult to visualize the lines described in Table E.3, the predicted lines represented in this table are presented in Figs. E.3 to E.8.

Discussion. It must be remembered that the data represent measurements over a 2-day period in the life of any one plant and are thus a "snapshot" of what that plant was doing during that period. The course of leaf development over a period of weeks was not followed; rather, development changes with age are inferred by comparing younger leaves with older leaves at the same time.

RATE OF LEAF PRODUCTION TEMP*VARIETY INTERACTION

Figure E.2. Interaction of temperature*variety on rate of leaf production.

Decline of relative growth rate C1-884

Figure E.3. Decline of relative growth rate with age for the variety C1-884. Leaf position is number of nodes from the top (< 3.5 cm).

Decline of relative growth rate C14-343

Figure E.4. Decline of relative growth rate with age for the variety C14-343. Leaf position is number of nodes from the top (< 3.5 cm).

Decline of relative growth rate Desiree

Figure E.5. Decline of relative growth rate with age for the variety Desiree. Leaf position is number of nodes from the top (< 3.5 cm).

Decline of relative growth rate Katahdin

Figure E.6. Decline of relative growth rate with age for the variety Katahdin. Leaf position is number of nodes from the top (< 3.5 cm).

Decline of relative growth rate LT-1

Figure E.7. Decline of relative growth rate with age for the variety LT-1. Leaf position is number of nodes from the top (< 3.5 cm).

Decline of relative growth rate Norchip

Figure E.8. Decline of relative growth rate with age for the variety Norchip. Leaf position is number of nodes from the top (< 3.5 cm).

Table E.3. Sequential mean and linear coefficients for the regression of leaf relative growth on leaf position.

Cultivar	Temperature					
	17C		22C		27C	
	mean*	slope*	mean	slope	mean	slope
C1-884	.200	-.0402	.226	-.0458	.176	-.0302
C14-343	.195	-.0419	.252	-.0554	.243	-.0412
Desiree	.204	-.0486	.242	-.0543	.196	-.0341
Katahdin	.209	-.0509	.248	-.0666	.206	-.0409
LT-1	.214	-.0492	.238	-.0468	.203	-.0415
Norchip	.212	-.0535	.279	-.0620	.183	-.0313

* mean and slope. Each pair of points represents measurements of 30-40 leaves.

In their model Ng and Loomis (1984) used the figure of 0.35 leaves per day, or about 2.4 leaves per week, as the maximum rate of leaf initiation. This is about half the maximum values observed here. While the rate of leaf appearance in this experiment is a measure of leaf unfurling rather than leaf initiation, one might argue that they are closely related and that the Ng and Loomis figure is low, at least for the period of rapid vegetative growth sampled here. Ng and Loomis indicated in their discussion that they chose one of the lower of the reported literature values; therefore, a higher value may be more appropriate.

The interaction of cultivar with temperature for leaf production rate seems to indicate that this might be a place to improve the modeling of varietal response to temperature. C14-343 and Katahdin were higher than the other cultivars at all temperatures. All cultivars increased between 17 C and 22 C, but C14-343 continued to increase its leaf production rate at the high temperature, while the other cultivars did not. C1-884 even decreased its rate of leaf production at the high temperature. LT-1 seemed to be less affected by temperature than the others. A similar pattern of rate of leaf production rate peaking near 20 C and falling off was described by Borah and Milthorpe (1962), who, however, did not observe the extent of temperature by cultivar interaction noted here.

The data for the means of the relative growth rates (Table E.3) are similar to the leaf production rate data (Fig. E.2) in that differences between cultivars were small at 17 C, all cultivars increased from 17 to 22 C, and the differences between cultivars became pronounced at 27 C. LT-1 again was the cultivar least affected by temperature. With the exception of LT-1, the relative ranking of cultivars at 27 C was the same for mean relative growth rate (Table E.3) as for rate of leaf production (Fig. E.2).

Figures E.3 to E.8 show that the average relative growth rate generally has an inverse relationship with its decline with age (leaf position from top). Although all cultivars seemed to have a slower decline of relative growth rate with leaf position at the higher temperature, correcting leaf

position for leaf age would make them more similar, since the high temperature leaves, with more rapid rates of unfurling, are chronologically younger than those at low temperature. Adjusting for chronological age would also show that the leaves in the cooler regime have more days at the higher growth rate, as is evidenced by bigger leaves in cooler temperatures. The relative growth rate data tend to confirm the observations by Borah and Milthorpe (1962) that rapid initial leaf expansion rates are accompanied by a faster decline of expansion rate with age, but that these factors are also genotype dependent.

Although the data were insufficient for estimates of maximum leaf relative growth rate for each cultivar, the maximum value of leaf relative growth rate would seem to be about the same as the value used by Ng and Loomis (1984) of $0.5 \text{ g g}^{-1} \text{ d}^{-1}$ for young shoots. It is possible, however, that further research would show differences among cultivars in this component. The Ng and Loomis EAGELG (effect of leaf age on fraction of leaf DW capable of growing--p. 31) figure indicates that they "age" their leaves slightly faster than was observed here. As indicated above, the youngest leaves measured here were about at the end of their period of logarithmic growth and at the period when relative growth rate begins to decline. This would put them at about day 6 or 7 on the EAGELG figure. Combining leaf position with leaf production rate for plants at the "optimum" temperature would indicate that they continue to grow for 12-13 days beyond the start of measurement in this experiment, or about to day 20 on the EAGELG figure.

Conclusion. The significant temperature X cultivar interaction is accounted for by the fact that, although differences among cultivars were small at 17 C, the cultivars C14-343 and Katahdin have higher rates of leaf production and relative growth rates at the 27 C temperature. The data provide information on leaf growth that can be used to improve the Ng and Loomis model.

3. Effects of heat stress on carbon translocation and partitioning of assimilates throughout the season (Greenhouse experiment, Israel)

A study of the effect of heat stress on carbon translocation, and partitioning of assimilates along the season, was studied in the 1986 greenhouse experiment in Israel.

Materials and Methods. First fully expanded leaves of Norchip and Desiree plants were fed $^{14}\text{CO}_2$, and analyses of the radioactivity in the treated leaf, tops of the plants, and tubers were made 24 hours after labeling. (Preliminary experiments indicated negligible radioactivity in leaves below the treated leaf.) Twenty-nine, 44, and 64 days after emergence, leaves were exposed to ^{14}C .

Results and Discussion. Export of ^{14}C from the source leaf was lower in the beginning of the season, as compared to the later stages of plant development. Fifty to 70% of the total radioactivity which was recovered in the plant was located outside the source leaf 44 days after emergence (Fig. E.9). No significant differences were observed between the varieties nor between the temperature regimes. Export of ^{14}C from the source leaf

declined slowly towards the end of the season. These results indicate that export of assimilates from the source leaf was not affected by the high temperature conditions.

High temperatures reduced significantly the partitioning of assimilates towards the tubers (Fig. E.10). This effect was more pronounced in Desiree than in Norchip. More ^{14}C was recovered in the stem as a result of heat stress. It must be emphasized that even in the control greenhouse, temperature regimes were above the optimum for growth and yield of potatoes.

4. The effects of day and night temperatures on carbon uptake, translocation, and its partitioning in three cultivars (Phytotron experiment, Israel)

Materials and Methods. Temperature regimes were 22/12 vs. 32/12 C (day/night) in order to study the effect of day temperature; and 27/12 vs. 27/22 C (day/night) in order to study the effect of night temperatures. Day-length was 8 hours in both experiments. Plants of Desiree, Norchip, and Up-to-Date were fed with 50 μCi $^{14}\text{CO}_2$. Translocation and partitioning were studied by the method described in the greenhouse experiment. Temperature treatments started when plants had 3-4 leaves and lasted 5-6 weeks until $^{14}\text{CO}_2$ labeling.

Results and Discussion. Export of assimilates from the source leaf was almost identical for all varieties and all temperature treatments. About 65% of the radioactivity was exported from the source leaf in a period of 24 hours (Fig. E.11). High day or night temperatures enhanced partitioning of assimilates towards the top of the plant. This effect was more pronounced in Up-to-Date than in Norchip (Fig. E.12). A significant reduction in ^{14}C partitioning to the tubers was observed under high temperature regimes. High temperature caused a reduction of assimilate partitioning to the tubers (Fig. E.13). Higher day temperatures exhibited a stronger effect than higher night temperatures in all varieties. Up-to-Date was the most sensitive to high temperatures, while only a slight effect was observed in Norchip. Partitioning of ^{14}C to the roots was affected only by higher day temperatures, whereas night temperatures had no effect on any of the three varieties (Fig. E.14). Higher day temperatures resulted in a significant increase in ^{14}C partitioning to the roots. More partitioning of ^{14}C to the stems was found under higher temperatures, and again Norchip was the least sensitive of the three varieties (Fig. E.15).

A different way of expressing the radioactive results is by relative specific activity (RSA):

$$\text{RSA} = (\text{dpm in organ/d.w. of organ}) / (\text{dpm in plant/d.w of plant})$$

This value expresses the relative sink strength of the organs in the plant. The prominent phenomenon is the effect of high temperatures on RSA in the tops (Fig. E.16). Higher day or night temperatures increased significantly the sink strength of the top as compared to the other plant organs. RSA of stems, roots, and tubers were not affected by different temperature regimes (Figs. E.17, E.18, and E.19).

Fig. E.9a. Partitioning to the stem, Greenhouse, 1986.
Percent from total export.

Fig. E.9b. Export from the source leaf, Greenhouse, 1986.
Percent of total radioactivity.

Fig. E.10a. Partitioning to the top, Greenhouse, 1986.

110

Fig. E.10b. Partitioning to tubers, Greenhouse, 1986.

Fig.E.11. Export from the source leaf.

a. Effect of day temperature.

b. Effect of night temperature.

Fig. E.12. Partitioning to the top.

a. Effect of day temperature.

112

b. Effect of night temperature.

Fig. E.13. Partitioning to the tubers.
a. Effect of day temperature.

Fig. E.14. Partitioning to the root.
a. Effect of day temperature.

b. Effect of night temperature.

a. Effect of day temperature.

b. Effect of night temperature.

Fig. E.16. Relative specific activity - top.

a. Effect of day temperature.

b. Effect of night temperature.

Fig. E.17. Relative specific activity - stem.
a. Effect of day temperature.

117

b. Effect of night temperature.

Fig. E.18. Relative specific activity - roots.
a. Effect of day temperature.

118

b. Effect of night temperature.

Fig. E.19. Relative specific activity - tubers.
a. Effect of day temperature.

b. Effect of night temperature.

5. Carbohydrate analysis and sucrose hydrolysis (Israel)

Materials and Methods. The radioactive carbohydrates in the tops and the tubers of the plants from the phytotron experiment (Chapter V-B2) were analyzed. Samples of 50 mg of the tissue dry weight were extracted for radioactivity measurements in the starch, sugars, and residue fractions. The sugar fraction was later separated into reducing sugars and sucrose, using thin layer chromatography.

Results and Discussion. An increase in the level of the labeled sugars and a decrease in the starch fraction were observed in Up-to-Date under the high temperature conditions (Fig. E.20). This phenomenon was not observed in Norchip. An analysis of the sugars in the tubers indicated an accumulation of sucrose in the tubers of Up-to-Date as a result of heat stress (Fig. E.20). No accumulation of sucrose was observed in the tubers of Norchip.

Sucrose is the main translocated sugar in the potato plant. Accumulation of the translocated sucrose in the tubers may suggest an inhibition of sucrose hydrolysis as a result of heat stress. Sucrose synthetase was found to be the main sucrose hydrolyzing enzyme in the tubers. Activity of sucrose synthetase was studied using sucrose and UDP as substrates. Heat stress caused a marked decrease in sucrose synthetase activity (Fig. E.21). This reduction was more pronounced in Up-to-Date, as compared to Norchip.

Heat stress caused an increase in radioactive labeling of the residue fraction from the top. This increase was significant in Up-to-Date but not significant in Norchip. The residue fraction is assumed to be related to cell wall components. The high level of ^{14}C located in the residue fraction of tops of Up-to-Date was accompanied by a decrease in the labeled sucrose and reducing sugars. These results suggest an increase in sucrose hydrolysis activity in the tops of Up-to-Date as a result of heat stress.

Sucrose hydrolysis activity in the tops was studied at pH 5 (related to acid invertase), using radioactive sucrose as a substrate. A significant increase in sucrose hydrolysis activity was observed in the tops of the plants as a result of heat stress (Fig. E.22). Approximately a three-fold increase in enzyme activity was observed in Up-to-Date when expressed per mg protein (Fig. E.22a), and a four-fold increase when expressed per g fresh weight (Fig. E.22b). A significant increase in sucrose hydrolysis under high temperature conditions was also observed in Norchip, but the increase was smaller than in Up-to-Date.

6. Effect of photoperiod and temperature on leaf starch accumulation (Cornell)

In the past decade, several authors have reported for at least eight annual species that plants respond to short days with an increased rate of starch synthesis (eg. Chatterton and Silviu, 1979a). The effect was reported to be based on duration of the photosynthetic period and not a classical photoperiod response affected by dim light (Chatterton and Silviu, 1979b). The list of species studied included types classified as short-day, day-neutral, and long-day with respect to flowering response.

Fig. E.20a. Carbohydrates in the tubers.

121

Fig. E.20b. Sugars analysis in the tubers.

Fig. E.21. Sucrose synthetase activity in tubers.

Fig.E.22. Sucrose Hydrolysis in the tops.

a. Expressed as invertase activity per mg protein.

b. Expressed as invertase activity per g fresh weight.

However, one might speculate that potato is an exception, since short days cause the formation of a very strong sink in potato, which might counter the tendency to make more leaf starch each day. Since potatoes respond to long days and warm temperatures in a similar manner, the effect of high growing temperature on leaf starch synthesis was also tested.

At the subcellular level, an objective of this study is to determine the role of the chloroplast in sucrose/starch partitioning in the source leaf. Although several studies have provided direct or indirect evidence for a chloroplastic role in determining partitioning of triose-phosphate to starch (eg. Robinson, 1984), most papers on the subject have focused on control systems within the cytoplasm (Stitt et al, 1984). If potato leaf starch synthesis behaves similarly to the other annual species in its photoperiod response, studies with isolated chloroplasts and cytoplasmic enzymes are planned to further examine this process.

Materials and Methods. For experiments 1-3 and the temperature experiments, small cut seed pieces were planted in Cornell mix A in trays in the greenhouse. When plants were 5-6 cm tall, uniform plants were lifted, the mother tuber removed (previous studies showed an effect of the mother tuber on leaf starch formation), and transplanted into 13 cm clay pots in Cornell mix A. Within a few days, plants were grouped according to size, randomized, and placed in growth chambers under long days (6 h dim incandescent + 12 h full light in Exp. 1, 10 h dim light + 10 h full light in Exp. 2, and 18 h full light in Exp. 3) to equilibrate. In experiments 4 and 5, plants were from plantlets from in vitro stem cuttings and were grown as described in Part E1. When plants were at the 6-7 leaf stage (after about one week), the different photoperiod treatments were begun. The treatments were: dim extension (as above in experiments 1 and 2, 8 h dim + 10 h full light in Exp. 3), and short day (12 h in Exp. 1, 10 h in experiments 2 and 3). Exp. 3 also included a long day (18 h full light) treatment. Two further experiments compared either dim extension (8 h dim light + 10 h full light) or short day (10 h) treatments to the 18 h long day treatment. The two temperature experiments used temperatures of 20 C (cool) and 30 C (hot), with a 12-h photoperiod.

Plants were equilibrated at the cool temperature until the beginning of treatment. Unless otherwise noted, the two cultivars used in both the photoperiod and the temperature experiments were LT-1 and Norchip. On the days indicated, the first lateral leaflet of each of a pair of plants in each block was harvested one-half hour prior to the end of the 12 h (Exp. 1) or 10 h (other experiments), quenched in liquid N₂, and lyophilized. On one or two sampling dates in most experiments, similar samples were also taken just prior to the beginning of the photoperiod. In Exp. 3, samples were also taken from all treatments just prior to the end of the 18-h treatment on the last day. Samples were ground and analyzed for starch using the method of Ou-Lee and Setter (1985).

Results.

1) Photoperiod. The results of experiments 1-3 were quite similar, with short day plants having 50% higher starch synthesis rates than plants in the dim-extension treatment by day 7 (Fig. E.23). The effect of photoperiod was significant at the $p = 0.01$ level in two of the experiments

Fig. E.23. effect of photoperiod
on leaf starch accumulation

average of three experiments (day 11 is from
two experiments and day 13 from one experiment
only).

on day 3 and in all experiments on day 7. Starch levels at the end of the night period were also significantly different, but were only 3-4% of the daytime high for LT-1 (and 6-8% for Norchip). In the only experiment to include all three photoperiod treatments (Exp. 3), starch synthesis rates were double and triple that of the long-day treatment for the dim-extension and short-day treatments, respectively, by day 7 (Table E.4).

Table E.4. Starch accumulation rates* after one week of photoperiod treatments.

Treatment	Cultivar	
	LT-1	Norchip
Long Day	5.4	6.9
Dim Extension	11.2	14.9
Short Day	18.1	21.2

*mg starch g (DW)⁻¹ h⁻¹

Experiment 4 showed no significant difference between the long-day and dim-extension treatments (cultivars Tomasa Condemayta, LT-1, and C1-884), while starch accumulation rates of short-day plants were more than double those of long-day plants by day 4 in Experiment 5. There was no significant cultivar X photoperiod interaction in any experiment.

2) Temperature. Starch accumulation rates were 24% lower in the high-temperature treatment than the cool-temperature treatment by day 3 (significant at $p = 0.01$) and this ratio was the same on day 7 (Fig. E.24). There was no temperature X cultivar interaction, nor was the level at the end of the night period affected (Table E.5).

Table E.5. Effect of temperature on starch levels* at the end of the dark period (day 8).

Treatment	Cultivar	
	Katahdin	Norchip
Cool	9.6	13.5
Hot	8.3	16.8

*mg starch g (DW)⁻¹

Discussion. The significant effect of a dim photoperiod extension in these experiments are counter to the conclusions of Chatterton and Silvius (1979b). It may be that potato is more sensitive than the species they used or that Chatterton and Silvius did not have enough replication to show significant differences. In the one plot in which they show data for all three types of photoperiod treatments, it appears that the short-day treatment is about 50% higher than the dim-extension treatment, just as was found here. It may be that their objective was to find the photoperiod

Fig. E.24. EFFECT OF TEMPERATURE ON
LEAF STARCH ACCUMULATION

average of two experiments

treatment which gave the lowest starch synthesis rates, which was the long-day (full light) treatment, consistent with our findings.

It appears noteworthy that potato also responds to short days with increased leaf starch synthesis rates, even though a strong sink (the tuber) is formed. By day 8 there were significant differences in numbers of underground tubers as well as tuberization ratings of leaf cuttings (data not shown); thus the observation period was sufficient for the development of these sinks. Therefore, control mechanisms within the leaf regulate carbon flow to maintain sufficient levels of substrate over the 24-h cycle, in spite of increased sink demand. The effect of short-day vs. dim-extension treatments here is especially interesting, since each had the same duration of photosynthetic period and the short-day plants were strongly induced to tuberize. Perhaps leaf chloroplasts are affected by short days in a similar manner as stolon/tuber amyloplasts, such that starch synthesis rates are increased. However, there are obvious differences, since over 90% of the leaf starch is re-mobilized during the dark period, while the tuber starch pool is not subject to significant turnover.

The potato leaves responded to high temperature in a similar manner to the dim-extension or long-day treatments with respect to leaf starch synthesis. Here, the lack of an effect of temperature on starch levels at the end of the dark period confirms the above observation that the level of leaf starch is regulated according to plant needs and is not simply an overflow pool which gradually accumulates under certain conditions. In all cases, over 90% of the starch formed during the day was re-hydrolyzed during the dark period.

In conjunction with the above experiments, a technique was developed to isolate intact potato chloroplasts with rates of CO_2 -dependent O_2 evolution of up to $90 \text{ } \mu\text{moles } \text{O}_2 \text{ mg chlorophyll}^{-1} \text{ h}^{-1}$. Further experiments utilizing potato chloroplasts in examining the question of sub-cellular regulation of intra-cellular photosynthate partitioning are pending.

F. Simulation Models (Cornell)

We have examined heat tolerant cultivars for traits that might be associated with their ability to out-yield ordinary cultivars at high temperatures. One way to assess the importance of such differences among cultivars is through the use of a physiological model. The most detailed and explanatory of the many models developed for the potato is the one by Ng and Loomis (1984), called POTATO. We have studied this model at great length. Potentially it appears to be very useful, but we have identified a number of problems that require correction. Some of the more interesting ones are described briefly below. We also present results from work with a less complex model (Fishman et al., 1984; 1985). The latter work was carried out at Cornell, but there was constant consultation with the originators of the model in Israel.

Stem density. In its original form, POTATO produced anomalous predictions for the effects of stem density. The sensitivity analysis by the authors showed that, according to the model predictions, a 20% decrease in stem density would bring about a 4.0% decrease in total dry matter on day 50 of the 1978 growing season at Aberdeen, Idaho, and a 13.6% decrease on

day 100. Although not stated in the text, yields were expressed as g per stem rather than as g per m². Clearly, this is counter-intuitive--surely wider spacings would produce higher yields per stem, even if (at spacings less than the optimum) lower yields per unit area. This is especially true when one considers that the model assumes both soil moisture and soil fertility to be optimal at all times, regardless of plant spacing.

The model produced the same type of results when run on our 1980 data set at Freeville, New York (Fig. F.1). Dry weight yields per stem of both leaves and tubers were higher at 15 stems per m² than at lower stem densities. Analysis of the problem showed that the anomaly lay in the area of water relations. We now understand what produces the effect, and we have developed two possible changes to correct the problem (Fig. F.1). In order to know which solution is physiologically "correct" we are carrying out a spacing experiment in the field this summer. The experiment is designed expressly to provide the data for deciding this issue.

Wind speed. A second anomalous prediction from the sensitivity analyses in the original model dealt with wind speed. A 20% increase in this input variable produced a 6% increase in total biomass on day 50, and a 7.2% increase on day 100. Likewise, a 20% decrease in wind speed led to a predicted decline in total biomass of 4.2% and 7.2%, respectively, on days 50 and 100. We found similar predictions on the effects of wind speed in running the model on our local weather at the Cornell farm (Table F.1). There is no logical reason why increasing the wind speed should increase yields. One might speculate that in nearly stagnant air a slight increase in wind velocity could be beneficial because of improved availability of CO₂; but the effects of CO₂ concentration are not included in the model, so this cannot be the explanation. It would certainly seem that transpiration would be more rapid with increasing wind speed, and that yields should suffer from increased water stress. As in the case of stem density, the problem appeared to lie with water relations; but it has proved more difficult to identify a solution for the wind speed problem. As a temporary expedient, we have eliminated wind speed as an input variable, setting it to the same value throughout the season.

Table F.1. Sensitivity of POTATO to wind speed, using weather data from 1980, Freeville, NY. Data are expressed as grams per stem.

	Percentage of actual wind speed		
	<u>33</u>	<u>100</u>	<u>200</u>
<u>Day 50 of simulation</u>			
Leaf dry mass	7.6	8.9	10.5
Stem dry mass	3.7	3.8	4.0
Tuber dry mass	8.7	10.5	9.8
Total dry mass	22.4	25.7	26.8
<u>Day 100 of simulation</u>			
Leaf dry mass	2.7	4.9	5.3
Stem dry mass	5.0	5.5	5.8
Tuber dry mass	43.8	49.6	49.4
Total dry mass	54.2	62.7	63.3

Fig. F.1. Simulations of biomass (leaves + stems + tubers) at differing stem densities by POTATO (Ng and Loomis, 1984) and by two modified versions. In version W the fraction of evapotranspiration (ET) that is transpiration is 1.0 at and above LAI = 3.6 and 0.0 at LAI = 0.0, with linear interpolation between these points. In version P the relationship between LAI and photosynthesis is changed to give a more convex curvature between LAI 0 and 5.

Temperature. All crop simulation models require weather data as the input information to drive the model. However, they differ widely in their requirements for the many parameters by which weather is measured, and in the time step needed in these weather data. Since it is impossible to supply continuous information concerning weather inputs, weekly, daily, or hourly integration time steps are often used. A large time step will enable a model to run more quickly, yet this speed may be at the cost of accuracy.

POTATO estimates hourly values of temperature by reading in daily temperature means and amplitudes. It then estimates hourly temperatures through the use of a sine curve. This reduces the time needed for the task of reading in temperature data, since only two points need to be entered for each day rather than 24 points. Another advantage is that hourly temperature data are often unavailable. However, it is fair to ask whether the accuracy of simulation would be improved through the use of actual hourly data. We therefore compared simulations made from recorded hourly temperatures with simulations produced through the use of the sine curve approximations.

The data set used for this comparison was from the 1985 growing season at the Cornell research farm, Freeville, New York. To simplify the coding changes the new version--Version H--ran on hourly temperatures actually recorded for air and soil. (As published, POTATO derives soil temperatures from air temperatures.)

Compared to the original model, version H provided greatly improved accuracy in hourly temperatures. We decided to try the opposite extreme as well--what would happen if the daily mean temperature was used for each hourly temperature, i.e., if the amplitude was set to zero? In Version C daily mean temperatures for air and soil were read in and remained constant for 24-hour periods. There was no hourly variation in temperature by either sine curve approximation or real hourly data.

The simulation of leaves (Fig. F.2A), stems (Fig. F.2B), and tubers (Fig. F.2C) with the use of the sine curve approximation for hourly temperature appeared to be a good technique, since the results were very similar to those using actual hourly temperature data. In all cases, the dry weights from the model with actual hourly temperatures were only slightly lower than those from the model which used the sine curve. This lends support to the time saving device of estimating hourly temperatures by reading in only daily means and amplitudes.

Similar conclusions were found by Elkinton and Ferro (1985), who used hourly inputs for dew point and wind run in addition to temperature. Using weather data from Amherst, Massachusetts, they found very close dry weight simulation curves for tubers and total plants using either the sine curve or hourly inputs.

Surprisingly, POTATO in its original form (the sine curve approximation) and Version C (constant temperatures throughout the day) also produced very similar predictions (Fig. F.2). This suggested that the sensitivity of POTATO to hourly temperature, real or synthesized, is quite low--a suggestion at odds with the overall sensitivity of the model to temperature (Ng and Loomis, 1984). Therefore POTATO and Version C were

Fig. F.2. Simulation of leaves with hourly temperature values (H),
 sine curve simulation of hourly temperature values (S),
 and using constant temperature for 24-hour periods (C).

Fig. F.3. POTATO (S) compared to constant temperature for 24-h period (C), 1980 season, Freeville, N.Y. 133

Fig. F.4. POTATO (S) compared to constant temperature for 24-h period (C), 1978 season, Aberdeen, Idaho. 134

Fig. F.5. Field data (x) for Russet Burbank, 1980 season, Freeville, NY, compared to POTATO simulation of leaves (a), stems (b), and tubers (c).

Fig. F.6. Field data (x) for Russet Burbank, 1981 season, Freeville, NY, compared to POTATO simulation of leaves (a), stems(b), and tubers(c).

Fig. F.7. Field data (x) for Russet Burbank, 1980 season, Freeville, NY, compared to simulation of leaves (a), stems (b), and tubers (c), by a version of POTATO modified as in Table F.2.

Fig. F.8. Field data (x) for Russet Burbank, 1981 season, Freeville, NY, compared to simulation of leaves (a), stems (b), and tubers (c), by a version of POTATO modified as in Table F.2.

compared with data sets for other years and another location.

Fig. F.3 shows the comparison for the 1980 growing season at Freeville. Unlike the 1985 season, there was a substantial difference between the two versions. As might be expected because of the greater amplitude for daily temperatures, even larger differences were obtained when the two versions were compared for the 1978 data set from Aberdeen, Idaho (the original data set used to develop the model.) Simulated values for leaves and tubers were substantially higher when the amplitude was set to zero (Fig. F.4A,C). The difference in stems was smaller, but in the same direction (Fig. F.4B).

Because actual soil temperatures were unavailable for the 1978 and 1980 data sets, it was necessary to derive them from air temperatures. To test whether this might explain the greater differences between the two versions, we modified Version C again on the 1985 data; but this time soil temperatures in both were derived from air temperatures (data not shown). There was essentially no change from the results shown in Fig. F.2. We conclude that although the sensitivity to hourly temperatures may be low in some seasons, differences in other seasons are great enough to warrant using the sine curve approximation.

Tuning. In its published form, POTATO underestimated total biomass when compared to 1980 field data from the Cornell research farm (Fig. F.5). Moreover, the predicted partitioning of assimilate to the various organs was incorrect. Leaves (Fig. F.5A) and tubers (Fig. F.5C) were in approximately the correct ratio to one another, but the predictions for stems (Fig. F.5B) were far too low. Simulations for the 1981 season were equally poor (Fig. F.6). To correct these two problems a long list of changes has been incorporated into the model (Table F.2). A few of these are arbitrary "tuning" changes to make predictions closer to field data; but most of the new opinions are based upon physiological data from the literature or from work on this project.

The most significant changes were in the way the model handles the partitioning of assimilates. Research in this project (Parts A, B, and E) and in the published literature has demonstrated that partitioning to tubers is strongly affected by photoperiod and temperature. These effects, inadequately modeled in the original version, have now been incorporated through a function defined as "degree of induction." Through this function short photoperiods and cool temperatures favor tuber initiation and growth. Cultivar differences can be readily incorporated in the future, as can the effects of such factors as physiological age of mother tuber and level of soil nitrogen.

The opinions will need to be refined as the model is tested against the other data sets from Part A, and tuning changes will certainly be required for other cultivars. However, we believe that we have enhanced the "transportability" of POTATO through the modifications already made.

The modified model is compared to field data for Russet Burbank (the cultivar used in developing POTATO) grown at the Cornell farm in 1980 (Fig. F.7) and 1981 (Fig. F.8). The former data were used for the tuning; the 1981 data were used as a first validation, after which minor adjustments were made. The predictions are much closer to the measured data than were

Table F.2. List of changes made to POTATO. This version of the model is tuned to the 1980 growing season at Freeville, NY. Unless otherwise stated, references to figures and equations are from Ng and Loomis, 1984.

Set wind speed to a constant value (125 km/day).

Set the dry matter fraction for tubers at 0.15 instead of 0.11.

Correct code so that when a leaf dies its water is lost to the plant.

The fraction of Evapotranspiration (ET) that is Transpiration (T) is 1.0 (all of ET is T) at and above LAI = 3.6, and 0.0 at LAI = 0.0, and is linearly interpolated between these values.

Percent cover (for calculation of diffusion resistance) is 100% at LAI = 3.6 instead of 2.5.

Mother tuber provides no reserves to stems and tubers.

Remove effect of photoperiodic induction on tuber initiation.

Reduce emergence weights of 3 above-ground internodes by a factor of 100.

Create an effect of photoperiod and temperature on degree of induction to tuberize, make tuber initiation and growth a function of this effect, and make associated changes, as follows:

- a) The effect is based on Fig. 5 of Ewing, 1981, and is inserted into equations 19 and 20, for tubers only.
- b) Move leaf, stem, and tuber lines in Fig. 8a to (2,0),(6,1).
- c) Move Effect of reserves on tuber initiation to (3,0),(7,1) (Fig. 10b).
- d) Disable Fig. 10a, Effect of reserves on number of tubers developing from stolons.

Set the potential node initiation rate (PNIR) to 0.6 instead of 0.35/day.

For branches only, set Effect of apex age on node initiation (Fig. 9a.) to (20,1),(30,0) instead of (15,1),(25,0).

Disconnect Fig. 9b, and initiate the first branch when the number of main stem nodes reaches 14.

Set the potential branch initiation rate (PBRIR) to 0.36 instead of 0.5/day.

Limit the total number of branches to 0.4 of the number of main stem nodes.

Main stem leaves die at a physiological age of 55.6 rather than 50 days.

Adjust the Effect of leaf age on photosynthesis (Fig. 5d., p. 27) from (83.,0.) to (83.,.37).

Change the interpolation between amounts of photosynthesis on clear and cloudy days to a convex curvilinear rather than a linear relationship.

those obtained from the model in its original form. In the near future, other data sets not used to tune the model will be used for validation. The model will also be modified for other cultivars. The principle investigator plans to spend part of his sabbatical leave with Dr. Loomis in the spring of 1988, continuing his work on POTATO. The growth analyses described in Part A and the physiological information developed in the rest of the project will provide a rich resource for future improvements.

Israeli model. This model was developed for Desiree grown in the Negev. It is an explanatory model, but with much less physiological detail than POTATO. We have modified the model to run on an IBM PC computer, and have tuned it to data sets with the Katahdin cultivar grown for four years at Freeville, NY (Figs. F.9-F.12) and for two years at the Cornell research farm at Riverhead, Long Island (Figs. F.13-F.14). The model should be easily adapted to the other cultivars and locations described in Part A.

G. Overall Summary and Conclusions

During the course of this research a large body of information has been accumulated on a common set of potato cultivars and their responses to heat stress. These cultivars come from highly diverse genetic backgrounds and include varying degrees of sensitivity to high temperatures. Many aspects of growth and development under varied environmental conditions and many physiological comparisons of different parameters and biochemical responses are included in this body of data.

Some of the growth analyses initiated in tropical locations are still underway. When they are completed, there will be a substantial basis for model development over a wide range of cultivars and environments. Even aside from modeling, there will be interesting information for crop physiologists. For example, the experiments in the hot greenhouses have already shown that Norchip, C14-343, and C1-884 have the ability to produce tuber yields under extreme heat stress. The superiority of these clones was associated not with greater biomass production, but rather with better partitioning of assimilate to tubers at the expense of the rest of the plant. [Part A]

The stage of plant growth during which heat stress was applied affected the degree to which growth was reduced. Total biomass was affected most when two weeks of heat stress was applied when plants were four weeks old, but partitioning to tubers was most affected when stress was applied two weeks earlier. [Part B]

Both high night temperature and high day temperature reduced yields. High night temperature decreased total biomass as well as partitioning to tubers. There was also a dramatic increase in specific leaf area with increasing night temperature, a parameter which is important in simulation modeling. High day temperatures generally increased leaf, decreased tuber, and decreased total dry weights. Overall morphology was also modified, with high temperatures increasing node number and decreasing tuber number. The degree to which temperature affected these variables depended upon both photoperiod and cultivar. Norchip was outstanding in its ability to produce tuber dry weight under stressful temperatures and daylengths. [Part B]

Fig. F.9. Field data (+) for Katahdin, 1980 season, Freeville, NY, compared to simulation of leaves (a), stems (b), and tubers (c) by a tuned version of the Israeli model (Fishman et al., 1984; 1985).

Fig. F.10. Field data (+) for Katahdin, 1981 season, Freeville, NY, compared to simulation of leaves (a), stems (b), and tubers (c) by a tuned version of the Israeli model (Fishman et al., 1984; 1985).

Fig. F.11. Field data (+) for Katahdin, 1982 season, Freeville, NY, compared to simulation of leaves (a), stems (b), and tubers (c) by a tuned version of the Israeli model (Fishman et al., 1984; 1985).

Fig. F.12. Field data (+) for Katahdin, 1985 season, Freeville, NY, compared to simulation of leaves (a), stems (b), and tubers (c) by a tuned version of the Israeli model (Fishman et al., 1984; 1985).

Fig. F.13. Field data (+) for Katahdin, 1984 season, Riverhead, NY, compared to simulation of leaves (a), stems (b), and tubers (c) by a tuned version of the Israeli model (Fishman et al., 1984; 1985).

Fig. F.14. Field data (+) for Katahdin, 1985 season, Riverhead, NY, compared to simulation of leaves (a), stems (b), and tubers (c) by a tuned version of the Israeli model (Fishman et al., 1984; 1985).

Either high air temperature or high soil temperature was damaging to tuber yields, and the combination was most deleterious. However, the mode of action seemed to be different. Only high air temperature affected the degree to which leaves were induced to tuberize as reflected in ability of leaves to produce tuberization on cuttings. High soil temperatures affected the expression of the induced state: even if leaves were exposed to conditions favorable to tuberization, high soil temperature prevented tuber formation in the soil. This effect of hot soils was not dependent upon the presence of roots, since it could also be seen in cuttings that lacked roots. Although high soil temperatures blocked the expression of the tuberization stimulus in the underground stolon, they did not block the passage of the stimulus through the stolon, as evinced by the formation of tubers in cool air at the tips of stolons that had emerged from hot soils. [Part B]

A new technique was developed in an attempt to find a rapid, reliable method to estimate the growth and maintenance respiration coefficients in different cultivars. The technique produced anomalous results, perhaps because of the interdependence of respiration and growth effects within young and old leaves on a given shoot. Thus the technique did not answer the questions whether there are genotypic differences in the maintenance and growth respiration components among potato cultivars and, if so, whether such differences contribute to heat tolerance. The results did, however, indicate that there are cultivar differences in temperature response for some physiological components which are reflected in altered estimates of the growth respiration coefficients and which are probably related to partitioning within the shoot. Experiments with the more traditional dark starvation technique for estimating maintenance respiration demonstrated differences among cultivars, but the relationship to yield and temperature performance is still difficult to assess. We plan to explore this problem by examining the growth analysis data for differences in cultivar response to different field environments. In combination with this we will use physiological models to assess the effects of varying the respiration coefficients. [Part C]

Acute heat stress dramatically reduced photosynthetic rates, but there was substantial recovery after as little as one day back at cooler temperatures. Under chronic heat stress the reduction in photosynthetic rates was much smaller or non-existent. Differences among cultivars in response to daytime temperatures did not appear to explain differences in heat tolerance. Stomatal resistance decreased with heat stress, indicating that any decline in photosynthesis was produced by increased mesophyll resistance. [Part D]

Although somewhat more pronounced at the higher temperatures, there was a steady decline in carbon dioxide fixation as leaves became older in both hot and cool temperature regimes. Photoperiod had a greater effect than did temperature on photosynthetic rates as leaves aged; short days hastened the decline with aging. [Part D]

In four "wild" Solanum species sensitivity to chronic heat stress, as reflected in reduced shoot growth, was associated with reduced efficiency of the light reaction of photosynthesis. The relationship was most apparent in older leaves. Preliminary experiments with these wild species suggested

that delayed fluorescence measurements may be useful in demonstrating differences in the response of the photosynthetic apparatus between heat tolerant and sensitive genotypes. It appeared that differences between tolerant and sensitive genotypes were more pronounced when older leaves were sampled. The advantage of measuring delayed fluorescence is that it is sensitive to metabolism on the oxidizing side of Photosystem II, whereas variable fluorescence is sensitive only to metabolic events on the reducing side of Photosystem II. [Part D]

The status of leaves with regard to degree of induction to tuberize (as reflected in tuberization of leaf-bud cuttings) was affected by both temperature and photoperiod. Lengthening the photoperiod from 10 to 16 h reduced induction more than did increasing the temperature from 20/15 C to 30/25 C, but cultivars differed in their responses. Temperature had little effect on Norchip's induction under 10-h days, but a large effect at 16 h. This information will be useful in modeling the interactive effects of photoperiod, temperature, and cultivar on partitioning of assimilate to tubers. Also useful in modeling will be the data on rates of leaf production and relative growth rates. Although differences among cultivars were small at 17 C, the cultivars Cl4-343 and Katahdin had higher rates of leaf production and relative growth rates at the 27 C temperature. [Part E]

Many of our experimental results have pointed to the importance of understanding differences in assimilate partitioning if we are to learn more about the physiology of heat tolerance in potato. Experiments with $^{14}\text{CO}_2$ indicated that export of assimilates from the source leaf was not affected by temperature or cultivar, but high temperatures reduced the partitioning of assimilates towards the tubers and increased partitioning to the shoot. The shifts in partitioning were more pronounced in the cultivars that were more sensitive to heat. Higher day temperatures exhibited a stronger effect on partitioning than higher night temperatures in all cultivars. Higher day temperatures resulted in a significant increase in ^{14}C partitioning to the roots. Expressing the radioactive results in terms of relative specific activity showed that the relative sink strength of the shoots increased at higher day or night temperatures. [Part E]

Interesting changes in carbohydrates were associated with heat stress. Leaf starch accumulation rates were depressed by 24% at high temperatures, and even greater differences in these rates were associated with photoperiod. Although extending the photoperiod with full light had the greatest effect, even a dim-light photoperiod extension depressed rates significantly. Moreover, the cultivar with the least sensitivity to photoperiod in tuberization response had higher rates than the more sensitive cultivar. An increase in the level of the labeled sugars and a decrease in the starch fraction at high temperatures were observed in tubers of the heat sensitive but not in the heat tolerant cultivar under heat stress. This accumulation of sugars was in the form of sucrose, not reducing sugars, which raised the possibility that heat stress inhibits sucrose hydrolysis in the tubers. Sucrose synthetase was found to be the main sucrose hydrolyzing enzyme in the tubers. Heat stress caused a marked decrease in sucrose synthetase activity, especially in the heat sensitive cultivar. [Part E]

Heat stress caused an increase in radioactive labeling of the residue fraction (presumably cell wall components) from the shoots, but only in the heat sensitive cultivar. This was accompanied by a decrease in the labeled sucrose and reducing sugars, suggesting an increase in sucrose hydrolysis activity in the shoots as a result of heat stress. A significant increase in sucrose hydrolysis activity was observed in the tops of the plants as a result of heat stress, especially in the heat sensitive cultivar. Thus heat stress of the sensitive cultivar was associated with increased sucrose hydrolysis of shoots and decreased sucrose hydrolysis in tubers, indicating that the activity of enzymes controlling carbohydrate status may play a key role in the effects of heat stress on the partitioning of assimilate in the potato. [Part E]

The physiological model "POTATO" was studied in great detail. Key problems have been identified and corrected, and the model has been tuned to upstate New York conditions. A framework has been established for tuning it to the tropics as well. The less complex model from Israel has also been tuned for New York. The growth analyses data and other physiological information obtained in this project have already been used to improve the models, and they provide a rich resource for further improvements. In turn sensitivity analyses with the models promise to help us understand more about the potential contribution of various physiological traits to heat tolerance. [Part F]

H. Acknowledgements.

The following graduate students contributed to the work of this project:

James Lorenzen (Cornell)
Matthew Reynolds (Cornell)
Richard Snyder (Cornell)
Shmulik Wolf (Rehovot)
Amnon Alesinski (Rehovot)

In addition, Mr. Wayne Heym and Mr. Joel Schusdek made valuable contributions to the computer modeling; and Mrs. T. Bloch was very helpful in carrying out the experiments in Israel.

I. Literature Cited.

- Amthor, J.S. 1984. The role of maintenance respiration in plant growth. *Plant, Cell, and Environ.* 7:561-569
- Amthor, J.S. 1986. Evolution and applicability of a whole plant respiration model. *J. Theor. Biol.* 122:473-490
- Ben Khedher, M. and E.E. Ewing. 1985. Growth analyses of eleven potato cultivars grown in the greenhouse under long photoperiods with and without heat stress. *American Potato Journal.* 62:537-554.
- Boodley, J.W. and R. Sheldrake, Jr. 1973. Cornell peatlite mixes for commercial plant growing. *Cornell University Information Bull.* 43.

- Borah, M.N. and F.L. Milthorpe. 1962. Growth of the potato as influenced by temperature. *Indian J. Plant Physiol.* 5:53-72.
- Chatterton, NJ and JE Silvius. 1979a. Photosynthate partitioning into leaf starch as affected by daily photosynthetic period duration in six species. *Physiol. Plant.* 49:141-144
- Chatterton, NJ and JE Silvius. 1979b. Photosynthate partitioning into starch in soybean leaves. I. Effects of photoperiod vs. photosynthetic period duration. *Plant Physiol.* 64:749-753
- Clegg, M.D., C.Y. Sullivan, and J.D. Eastin. 1978. A sensitive technique for the rapid measurement of carbon dioxide concentration. *Plant Physiol.* 62:924-926
- Ellenson, James L. 1986. Flash-induced delayed light emission patterns of red kidney bean leaves: Evidence of a new component dependent upon tissue integrity. *Plant Physiol.* 80: 988-991.
- Ewing, E.E. 1981. Heat stress and the tuberization stimulus. *American Potato Journal.* 58:31-49.
- Ewing, E.E. 1985. Chapter 5. Cuttings as simplified models of the potato plant. In: Li, P.H. (Ed.): *Potato Physiology*. Academic Press, Orlando, Florida. pp. 154-207.
- Ewing, E.E. and P.F. Wareing. 1978. Shoot, stolon, and tuber formation on potato (*Solanum tuberosum* L.) cuttings in response to photoperiods. *Plant Physiol.* 61:348-353.
- Fishman, S., H. Talpaz, M. Dinar, M. Levy, Y. Arazi, Y. Rozman and S. Varshavsky. 1984. A phenomenological model of dry matter partitioning among plant organs for simulation of potato growth. *Agric. Sys.* 14:159-169.
- Fishman, S., H. Talpaz, R. Winograd, M. Dinar, Y. Arazi, Y. Roseman and S. Varshavski. 1985. A model for simulation of potato growth on the plant community level. *Agric. Sys.* 18:115-128.
- Irving, D.E. and J.H. Silsby. 1987. A comparison of the rate of maintenance respiration in some crop legumes and tobacco determined by three methods. *Ann. Bot.* 59:257-264
- Krause, G.H. and E. Weis. 1984. Chlorophyll fluorescence as a tool in plant physiology. II. Interpretation of the fluorescence signals. *Photosynthesis Research* 5: 139-157.
- Lambers, H., R.K. Szaniawski, and R. de Visser. 1983. Respiration for growth, maintenance, and ion uptake. An evaluation of concepts, methods, values, and their significance. *Physiol. Plant.* 58:556-563
- Lechowicz, M.J. and L.E. Hellens. 1980. Latitudinal trends in the responses of growth respiration and maintenance respiration in the beach pea, *Lathyrus japonicus*. *Can. J. Bot.* 58:1521-1524

- Manrique, L.A. and R. Meyer. 1984. Effects of soil mulches on soil temperature, plant growth and potato yields in an aridic isothermic environment in Peru. *Turrialba*. 34(4):413-420.
- McCree, K.J. 1974. Equations for the rate of dark respiration of white clover and grain sorghum, as functions of dry weight, photosynthetic rate, and temperature. *Crop Sci.* 14:509-514
- McCree, K.J. & J.H. Silsby. 1978. Growth and maintenance requirements of subterranean clover. *Crop Sci.* 18:13-18
- Midmore, D.J. 1984. Potato (*Solanum* spp.) in the hot tropics I. Soil temperature effects on emergence, plant development and yield. *Field Crops Research*. 8(1984):255-271.
- Midmore, D.J. and H.A. Mendoza. 1984. Improving adaptations of the potato (*Solanum* spp.) to hot climates - some physiological considerations. Proceeding: 6th Symposium of the International Society for tropical root crops. (CIP). Lima, Peru. pp. 457-464.
- Ng, E. and R.S. Loomis. 1984. Simulation of growth and yield of the potato crop. *Simulation Monographs*. Pudoc, Wageningen.
- Ou-Lee, TM and TL Setter. 1985. Enzyme activities of starch and sucrose pathways and growth of apical and basal maize kernels. *Plant Physiol.* 79:848-851
- Pearcy, R.W. 1977. Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentiformis* (Torr) Wats. *Plant Physiol.* 59:795-799
- Papageorgiou, G. 1975. Chlorophyll fluorescence: An intrinsic probe of photosynthesis. In: *Bioenergetics of photosynthesis*. Govindjee ed., Academic Press. New York. pp. 320-366.
- Rasco, E.T., Jr., R.L. Plaisted, and E.E. Ewing. 1980. Photoperiod response and earliness of *S. tuberosum* ssp. *Andigena* after six cycles of recurrent selection for adaptation to long days. *Am. Potato J.* 57:435-448.
- Reynolds, M.P. and E.E. Ewing. 1986. Screening accessions from the IR-1 potato collection for heat tolerance. (Abs.) *Amer. Potato J.* 63: 451.
- Robinson, JM. 1984. Photosynthetic carbon metabolism in leaves and isolated chloroplasts from spinach plants grown under short and intermediate photosynthetic periods. *Plant Physiol.* 75:397-409
- Smillie, Robert M., Suzan E. Hetherington, C. Ochoa, and P. Malagamba. 1983. Tolerances of wild potato species from different altitudes to cold and heat. *Planta* 159: 112-118.
- Stitt, M, B Kuerzel, and HW Heldt. 1984. Control of photosynthetic sucrose synthesis by fructose 2,6-bisphosphate. II. Partitioning between sucrose and starch. *Plant Physiol.* 75:554-560

Szaniawski, R.K. and M. Kielkiewicz. 1982. Maintenance and growth respiration in shoots and roots of sunflower plants grown at different root temperatures. *Physiol. Plant.* 54:500-504

Van der Zaag, D.E. 1984. Reliability and significance of a simple method of estimating the potential yield of the potato crop. *Potato Research.* 27:51-73.

Wilson, D., and J.G. Jones. 1982. Effect of selection for dark respiration rate of mature leaves on crop yields of Lolium perenne cv S23. *Ann. Bot.* 49:313-320

IV. DESCRIPTION OF COOPERATION

Throughout this project there has been frequent communication and close coordination of efforts. Communication was by mail, BITNET computer mail, long distance telephone, exchange of personnel, and other personal visits. All phases of the research--planning, carrying out the experiments, and interpretation of the results have been shared between the two locations. Not only has this close cooperation been of great benefit to the research at both locations, it has fostered the development of warm friendships that will certainly lead to future collaboration among scientists at the two locations.

Concrete examples of cooperation are:

- A. Heat tolerant clones selected at Cornell were sent in vitro to Israel for multiplication and subsequent experimentation. In this way the same genetic material could be investigated at both locations.
- B. Dr. Ewing made two visits to Israel, and Dr. Dinar visited Cornell. Planning conferences were held among the investigators during each visit, and research results were discussed in depth.
- C. Mr. Shmulik Wolf, graduate research assistant working on the project in Israel, made two visits to Cornell while en route to other locations. During these visits he was made familiar with techniques and facilities being used for the project at Cornell.
- D. Prof. Hovav Talpaz, one of the developers of the Israeli simulation model, also visited Cornell and helped transfer the model to the Cornell computer. Later Mr. Joel Schusdek spent a year at Cornell, devoting all of his time to the Israeli model. During his visit, Mr. Schusdek conferred regularly via BITNET with Drs. Talpaz and Fishman in Israel.

In addition to cooperation among the investigators who were part of this project, there were also useful linkages to other projects. Through coordination with the International Benchmarks Sites Network for Agrotechnology Transfer (US AID Contract No. DAN-4054-C-00-2071-00) the same set of clones grown in Israel and New York were planted at three elevations in Maui, Hawaii, for growth analyses in both 1985 and 1986. These and similar cooperative experiments in Peru, Tunisia, and the Philippines will constitute substantial additions to the data base for model development.

V. EVALUATION OF THE RESEARCH ACHIEVEMENTS

Objective A: Growth Analyses on a Common Set of Potato Cultivars

Cultivars from a range of genetic backgrounds, representing varying degrees of sensitivity to high temperatures, were multiplied in vitro and distributed in that form or as tubers to Israel and other warm locations. (Most of the field experiments at other locations were supported largely by cooperating agencies, including US AID and the International Potato Center.) Some of the growth analyses initiated in tropical locations are still underway, but ten replicated field experiments with the cultivars have already been harvested. In each of these experiments there were at least three biomass harvests (leaves, stems, and tubers separately) plus a final tuber harvest, all according to a common protocol. Hourly meteorological data were collected in each. The combined data sets will comprise a very useful data base for development of potato growth models over a wide range of environments and germ plasm. To help interpret the field studies, similar experiments were carried out in greenhouses at both Cornell and Rehovot.

The work under this objective has gone very well overall. Because many of the clones and cultivars used in the experiments are unavailable from commercial sources at any given location, it was necessary to go through the laborious process of in vitro multiplication, followed by further multiplication in greenhouses, screenhouses, or field locations which were not subject to aphid infestation. However, the extra effort was beneficial in that all of the seed tubers in a given experiment had a common history; and because of these procedures it was possible to test the same set of cultivars in highly diverse environments. The resulting data will be of interest not only to modelers, but also to other crop physiologists who are concerned with genotype X environment interactions.

Objective B: Physiological Bases for Cultivar Differences in Response to Heat Stress

Research under this objective examined many aspects of cultivar response to heat stress. Responses to high air temperatures and high soil temperatures were compared. Heat stress during the day was contrasted with heat stress at night, and interactions with photoperiod were studied. Measurements of dark respiration and photosynthesis revealed interesting differences among cultivars in their responses to heat stress, and these results have opened up possibilities that should be pursued in future research. Differences in partitioning of assimilate to various organs stood out as the most clear cut distinction among cultivars in their response to heat stress. The differences in intracellular and inter-organ partitioning of carbohydrates were especially noteworthy, and open exciting insights into the role of sucrose and enzymes controlling its metabolism in the growth and development of the potato.

The results from this objective, coupled with the growth analyses data, also present a great deal of information that can be used in improving potato models.

Objective C: Use the Information from the First Two Objectives to Improve the Modeling of Growth and Development in the Potato

Much work remains before this objective will be completed, but much has already been accomplished. The physiological model "POTATO" was studied in great detail. Key problems were identified and corrected, and the model was tuned to upstate New York conditions. A framework has been established for tuning it to the tropics as well. The less complex model from Israel has also been tuned for New York. A small amount of the information from the growth analyses has been used to improve the models, but most of the data sets are being saved until tuning to New York conditions has been completed for each cultivar. Information on plant development rates and other physiological information from the work on the second objective has been used to modify opinions contained in POTATO and to develop new opinions that improve its ability to simulate partitioning of assimilate.

Sensitivity analyses with the models promise to help us understand more about the potential contribution of various physiological traits to heat tolerance. This could provide new insights to plant breeders as to ideotypes best suited to particular locations. Other uses of the models will be for crop management, including decisions on optimal dates for harvest and planting, integrated pest management (when linked to appropriate pest models), and cultivar selection.

VI. LIST OF PUBLICATIONS

- Ewing, E.E., M. Ben Khedher, E.J. Batutis, R.G. Snyder, and G.W. Fick. 1984. Partitioning of dry matter in the potato--implications for modeling. In Abstracts of conference papers of the 9th triennial conference of the EAPR, F.A. Winiger, ed. European Association for Potato Research, Interlaken. p. 344-5.
- Ewing, E.E. 1986. Potato sets and potato models. In Proceedings of the joint U.S.-Israel workshop on development of computer supported agricultural extension. Y. Elkana, ed., Ministry Agriculture Extension Service, Tel-Aviv, Israel and U.S. Dept. Agriculture Extension Service, Washington, D.C. p. 195-203.
- Lorenzen, J.H. 1986. Differences among potato (Solanum tuberosum L.) varieties in effects of temperature on respiration and growth. M.S. Thesis, Cornell University. 72 pp.
- Lorenzen, J.H., R.A. Alscher, and E.E. Ewing. The effect of daylength on daily starch accumulation in potato. (abs.) Amer. Potato J. (Submitted).
- Lorenzen, J.H., R.A. Alscher, and E.E. Ewing. The effect of photoperiod on daily starch accumulation in potato. (abs.) Amer. Soc. Hort. Sci. (Submitted).
- Lorenzen, J.H. and E.E. Ewing. 1986. Determining growth and maintenance respiration in potato leaves. (abs.) Amer. Potato J. 63:440.
- Reynolds, M.P. and E.E. Ewing. 1986. Effects of air and soil temperatures on potato tuberization. (abs.) Amer. Potato J. 63:451.
- Reynolds, M.P., E.E. Ewing, and T.G. Owens. Heat tolerance in wild potato species: Its relationship with photosynthetic capacity and leaf age. (abs.) Plant Physiol. (Submitted).
- Snyder, R.G. 1987. Heat tolerance, growth analysis, and computer simulation of growth and dry matter partitioning in the potato. Ph.D. Thesis, Cornell University. 246 pp.
- Snyder, R.G. and E.E. Ewing. 1986. Simulation modeling and growth analysis in the potato. (abs.) Amer. Potato J. 63:456.