REDUCTION IN POTATO GROWTH AT HIGH TEMPERATURE: ROLE OF PHOTOSYNTHESIS AND DARK RESPIRATION

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Abstract

The relationship of photosynthesis and dark respiration to reduced potato growth at temperatures above 20°C was determined. Ten potato clones were propagated *in vitro* from sterile plantlets and grown in a growth chamber at 20/15°C and 30/25°C (day/night) with an 18 hr. daylength. Plants were harvested 26 to 30 days after transplanting. Daylength was decreased to 12 hrs. to induce tuberization and plants were harvested at 45-51 and 75-79 days after transplanting. At each harvest one plant from each cultivar was chosen from each of five blocks and selected growth (tuber number and dry weight of leaves, stems, roots and stolons, and tubers) and physiological variates [leaf area, net photosynthesis, maintenance dark respiration, and chlorophyll fluorescence parameters 0 (Initial), P (Peak), T (Terminal), P-O (Variable fluorescence) and P-T (Fluorescence quenching)] were measured. The high temperature decreased root and stolon, tuber and total dry weight and increased stem dry weight. Amongst physiological variates, the higher temperature decreased leaf area, net photosynthesis and maintenance dark respiration. The chlorophyll fluorescence parameter 0 significantly increased, which also increased the P and T parameters. Variable fluorescence (P-O) and fluorescence quenching (P-T) were not significantly affected by the growth temperature. The analyses of covariance, in which physiological variates were used as covariates to remove significant differences in growth variates, indicated that the most effective covariate was the T chlorophyll fluorescence parameter. The least effective covariates were leaf dark respiration and the chlorophyll fluorescence parameters P-O and P-T. The changes in 0 fluorescence suggest that reduced photosynthetic efficiency, particularly in Photosystem II, plays a major role in reduced potato production at high temperatures.

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Introduction

The potato (*Solanum tuberosum* L.) is well adapted to mean temperatures of 17°C (4). Higher temperatures, like those encountered in the tropics and subtropics, cause severe yield decreases (15) and are considered a major environmental constraint for potato production. Reduced yields at high temperature are due in part to reduced production of assimilates, and reduced tuber initiation and partitioning of assimilate to tubers (tuber bulking) (7). In most of the currently available cultivars, tuber initiation and bulking are favored by temperatures below 20°C (7). Temperatures in excess of 18-20°C tend to stimulate haulm growth and depress both tuber initiation and bulking (1, 2, 4, 13). Temperatures above 29°C can reduce leaf area and weight suffficiently to stop tuber production (4).

Processes altered by temperature may include one or more of the following: Photosystem I (PS I), Photosystem II (PS II), Calvin cycle, photorespiration, dark respiration, carbohydrate translocation and reduced leaf area (less light interception). There have been some successful efforts to identify heat tolerance at the chloroplast level (Photosystem-Calvin cycle) using the chlorophyll fluorescence technique (9, 20), but the results have not been adequately compared with the growth response of the plants. Bushnell (4) provided data on potato respiration and photosynthesis between 20 and 29°C that suggested dark respiration would continue to increase with temperature, whereas photosynthesis would decline. Increasing dark respiration and declining photosynthesis rates resulted in net leaf assimilation falling to zero at about 36-38°C (23, 24). These results led Burton (3) to propose that above 30°C net assimilation in whole potato plants drops to zero.

The dark respiration of whole plants is now considered to be composed of two components, growth and maintenance respiration (18). Growth respiration, which utilizes respiratory substrate to produce dry matter and is dependent on the tissue chemical composition, predominates in meristematic regions and is generally ignored in measurements of mature carbohydrate-exporting leaves at steady-state (18). Maintenance respiration, which represents the energy required to maintain the biomass, probably depends on the tissue composition and the growth environment, particularly temperature (11). The higher the temperature, the shorter the half-lives of enzymes, membranes, and other macromolecules, and the greater the demand for maintenance respiration (18).

The maintenance component is generally believed to be more responsive to selection than growth respiration (14, 22). In ryegrass, plants selected for slower rates of dark respiration in mature leaves have significantly higher rates of biomass increase (5, 22). This biomass increase is not related to the photosynthetic rate or photorespiration rate (22). Wivutvongvana (25) compared heat-sensitive and heat-tolerant clones of *Solanum chacoense* Bitt. and *S. acaule* Bitt. and observed higher dark respiration in the sensitive clones.

Selections for heat tolerance in the field did not have higher photosynthetic rates under heat stressed conditions (25). These studies indicate the need to further examine the relationship between maintenance dark respiration and heat tolerance in potato.

The purpose of this study was to measure selected physiological variates (maintenance dark respiration, net photosynthesis, leaf area, and chlorophyll fluorescence parameters) and compare their ability to explain significant temperature effects on potato yield components (dry weight of leaves, stems, roots and stolons, and tubers).

Materials and Methods

Plant Material: Ten potato (*Solanum tuberosum* L.) cultivars were used in the experiment: A14-0-11, Atlantic, Bintje, C14-343, Desiree, DTO-33, LT-1, Norchip, Red Pontiac, and Russet Burbank. Plants were propagated *in vitro* using nodal cuttings from aseptic tissue-cultured parent material. Following standard sterile protocol, 10-12 nodal cuttings were placed into plastic Magenta GA7 vessels (Magenta Corp., Chicago, U.S.A.) with 60 mL of Potato Nodal Cutting Media containing the following (g/L): Murashige and Skoog salts, 4.3; monobasic sodium phosphate, 1.02; thiamine HCl, 0.0004; i-inositol, 0.1; sucrose, 30; agar, 6. There were three Magenta vessels for each of the 10 cultivars for a total of 30-35 nodal cuttings per cultivar. The Magenta vessels were placed in a tissue culture growth room under low light from fluorescent lamps (150-200 μmol $m^{-2}s^{-1}$, 16 hr. daylength) at *ca.* 24°C day/18°C night.

Plant Growth Measurements: After *ca.* four weeks, when the plantlets were at the 4-5 leaflet (5 mm or longer) stage, 25 of the most uniform plantlets of each cultivar were transplanted to 10 cm standard plastic pots with a planting medium containing equal volumes of coarse vermiculite, perlite, and Nova Mix 200-Peat Lite Mix. The plants were placed in a Conviron PGV36 walk-in growth chamber under a combination of fluorescent (75%) and incandescent (25%) lights (*ca.* 300 μmol $m^{-2}s^{-1}$, 18 hr. daylength) at 20°C day/15°C night temperature, measured at the top of the plant canopy, and 70-80% R.H.

After *ca.* one week, 15 uniform plants of each cultivar were randomized into five blocks of three plants each and all 150 plants were placed in the same growth chamber. All plants were watered with ½ strength Hoagland and Arnon solution (10) once a week and with tap water as required.

Twenty-six to 30 days after transplanting, "vegetative period" measurements were taken on each cultivar. One plant from each cultivar was chosen from each of the five blocks and measured for leaf maintenance dark respiration; net photosynthesis; chlorophyll fluorescence parameters 0, P and T; leaf area; tuber number; and leaf, stem, root and stolon, and tuber dry weight.

On day 31, the daylength was shortened to 12 hrs. to induce tuberization. At 45-51 days, when the plants were in the early stages of tuber production, a second harvest of five plants of each cultivar was taken. The final harvest, of five plants of each cultivar, was taken at 75-79 days.

The growth chamber temperature was increased to 30°C day/25°C night and the experiment was repeated with a second set of plants as described above.

Physiological Measurements: At each sampling time, plants were measured one block per day for a total of 5 days. In order to estimate maintenance dark respiration without any growth respiration, the plants were held in darkness in the lab for 24-32 hrs. before being measured for maintenance dark respiration (11) and net photosynthesis. The respiration and photosynthesis measurements were taken on the terminal leaflet of the most recently fully-expanded leaf, held in a temperature-controlled Plexiglas leaf curvette, at 20°C and 30°C leaf temperature for the first and second set of plants, respectively. The air entering the cuvette was atmospheric air which had a dew point of 5°C. The carbon dioxide flux was measured on an ADC MK3 IRGA. After the maintenance dark respiration measurement the cuvette was exposed to two high pressure sodium lamps, which provided 400 μmol $m^{-2}s^{-1}$, as measured by a Li-Cor Li-190S quantum sensor and the net photosynthetic rate was recorded.

Chlorophyll fluorescence measurements were taken the next day; plants were held for at least 1 hr. at the growing temperature. The measurement was taken on the same leaf that was used for gas exchange measurements using a Plant Productivity Fluorometer Model SF-20 (Richard Brancker Research, Ottawa, Ontario, Canada). The SF-20 sensor was placed firmly on the upper surface of the leaf, avoiding the mid-vein, and the initial (O), peak (P), and (after 50 s) the terminal (T) values of the chlorophyll induction curve were recorded from the SF-20 digital display. Variable fluorescence (Fv) was calculated as the difference between P and O, while the difference between P and T estimated fluorescence quenching [see 12, 16 for a review of fluorescence induction (Kautsky effect)].

After the chlorophyll fluorescence measurements were completed, total leaf area was recorded with a Li-Cor Li-3100 Leaf Area Meter. The plants were separated into four components; (1) leaves, (2) stems, (3) roots and stolons, and (4) tubers, oven-dried and weighed. Total plant dry weight was calculated as the sum of the leaf, stem, tuber, and root and stolon dry weights. In order to normalize the data, tuber number and dry weight growth variates were transformed to square root and log values, respectively, before analysis.

Statistical Analysis: Analyses of variance and covariance were conducted using the ANOVA directive of GENSTAT 5 (8). Analyses of variance were conducted first on the growth variates (total dry weight, tuber number, tuber dry weight, leaf dry weight, stem dry weight, and root and sto-

lon dry weight) and physiological variates [leaf dark respiration, leaf net photosynthesis, leaf area, and chlorophyll fluorescence parameters (O, P, T, Fv, and P-T)] in order to determine the effect of cultivar, temperature and harvest date. Analysis of covariance was done on each of the growth variates using the physiological variates singly as covariates. When a significant mean square value in the analysis of variance of the growth variates was non-significant after adjustment with a physiological variate, then the significant changes in growth variate could be explained by the concomitant (or covarying) changes in the physiological variate (21).

Results and Discussion

Physiological Variates: Temperature and harvest had an interactive effect ($P<0.05$) on leaf maintenance dark respiration (Table 1), determined on a leaf area or leaf dry weight basis (not shown). The response was always lower at the higher growth temperature and declined over the three harvest dates, in particular between harvest one and two. This reduction in maintenance dark respiration at 30°C was unexpected. Previous respiration measurements by Bushnell (4) and Winkler (23, 24) showed a respiration increase between 20 and 30°C. Because their measurements were done on leaves that had not been held in the dark for an extended period of time, their measurements would have included both growth and maintenance respiration components. A possible explanation for the declining respiration in this study is that the continuous high temperature had altered the availability of respiratory subtrates, resulting in fewer cells capable of maintenance respiration. This phenomenon warrants further study.

Leaf net photosynthesis was affected by the growth temperature and harvest date in combination (Table 1) and depended on cultivar. At 20/15°C net photosynthesis peaked at the second harvest date and it was always higher than at 30/25°C, regardless of the harvest date. At 30/25°C, the highest net photosynthesis rate was at the first harvest and declined throughout the growing period. These results are in complete agreement with previous research on temperature effects on leaf net photosynthesis of potato (3). Among the cultivars, C14-343 had the highest and Norchip had the lowest leaf net photosynthesis (Table 1).

All of the chlorophyll fluorescence variates, except P-T, depended on both temperature and harvest time (Table 1). Variates O, P and T were always lower at 20/15°C than at 30/25°C but increased over the growing season, while those at 30/25°C declined. The O and T values were less variable (by a factor of three) than P and consequently P-O and P-T. Therefore P-O (Fv) and P-T (an estimator of fluorescence quenching) were not useful in this study as covariates.

Variable fluorescence, Fv (P-O), was not affected as much by temperature and harvest as the O, P and T values. At 20/15°C, the Fv values in-

TABLE 1.—*Effect of cultivar, temperature and harvest on physiological variates.*

Treatment	Leaf resp.[1] (μmol CO_2 $m^{-2}s^{-1}$)	Leaf photo. (μmol CO_2 $m^{-2}s^{-2}$)	Leaf area (cm^2)	Chlorophyll fluorescence O	P	T
Cultivar (C)						
A14-0-11	0.773	8.21	119.2	92.6	138.7	103.4
Atlantic	0.908	6.68	159.0	79.6	123.8	92.9
Bintje	0.751	7.71	124.4	84.8	129.0	97.2
C14-343	0.686	9.36	109.0	88.4	136.6	104.7
Desiree	0.860	7.59	140.0	82.4	130.8	96.2
DTO-33	0.659	7.39	151.2	85.0	131.4	96.9
LT-1	0.828	7.74	129.8	83.5	129.8	98.1
Norchip	0.680	6.91	141.4	81.3	128.4	94.6
Red Pontiac	0.597	7.76	136.6	84.9	134.4	99.0
Russet Burbank	0.630	7.73	169.2	87.3	142.7	100.6
SEM (n=6 df=18)	0.0690	0.427	7.11	1.40	4.16	1.14
Temperature (T)						
20/15	0.801	9.20	150.0	55.5	104.9	69.9
30/25	0.674	6.22	126.0	114.5	160.2	126.8
SEM (n=30 df=18)	0.0308	0.191	3.18	0.63	1.86	.51
Harvest (H)						
1	0.972	8.27	91.7	91.9	135.1	109.5
2	0.634	8.27	166.9	79.9	129.6	94.1
3	0.606	6.58	155.4	83.1	133.0	91.5
SEM (n=20 df=18)	0.0378	0.234	3.89	0.77	2.28	0.62
T x H						
20/15						
Harvest 1	1.122	9.25	105.8	51.4	91.6	66.0
Harvest 2	0.641	10.49	171.3	52.9	104.0	68.9
Harvest 3	0.639	7.86	172.8	62.1	119.2	74.8
30/25						
Harvest 1	0.821	7.28	77.5	132.4	178.7	153.0
Harvest 2	0.628	6.06	162.4	106.8	155.1	119.2
Harvest 3	0.572	5.30	138.0	104.2	146.8	108.1
SEM (n=10 df=18)	0.0534	0.331	5.50	1.08	3.23	0.88
Sig. effects[1]	T*H	C,T*H	T,C*H	C,T*H	T,TxH	C,T*H

[1]Factorial effects: Interactions are denoted by "x" while "*" denotes all main and interactive effects are significant ($P<0.05$).

creased with harvest but at 30/25°C the Fv values did not change significantly with harvest. Fluorescence quenching, estimated by P-T, was significantly affected only by harvest time. These chlorophyll fluorescence results are very similar to previous research using the same instrumentation and a growing period of 28 days at 35°C (19). Schreiber and Berry (17) reported fluorescence yield increases with increasing degree of heat damage to the photosynthetic apparatus. An increase in Fv would result from inhibition on the photo-reducing side of PS II (20) and if there is thermal damage to PS II, there will be a dramatic increase in O (12). The initial fluorescence (O) is thought to represent emission by excited antenna chlorophyll *a* molecules occurring before the excitons have migrated to the reaction centers (12). Since the Fv chlorophyll fluorescence was slightly increased by temperature, there is some reason to suspect high temperature did reduce electron flow through PS I and the Calvin cycle. However, the increase in O, which was also a major contributor to the increase in the P and T values, was considerably more than the Fv increase. This strongly suggests that high temperature caused some disruption in the photosynthetic apparatus, primarily within PS II and not in PS I or the Calvin cycle.

Growth Variates: Both tuber number and dry matter components were influenced mainly by cultivar, temperature and harvest effects and by the interaction between temperature and harvest (Tables 2, 3, 4, 5).

There was a strong interaction between temperature and harvest on tuber dry weight (Tables 2, 3). Tuber dry weight at 30/25°C was always much lower than at 20/15°C and the differential depended on harvest dates. Use of the O, P or T fluorescence value was effective in removing the temperature effect and interaction with harvest on tuber dry weight. T fluorescence also removed the effect of harvest. The three cultivars with the highest tuber dry weight at 20/15°C (C14-343, Norchip, and Bintje) (Table 2) had the highest tuber number and lowest root and stolon dry weight. A similar relationship existed at 30/25°C for the three cultivars with the highest tuber dry weight (C14-343, Norchip, and A14-0-11).

For total dry weight the significant effects of temperature and harvest were reduced by the physiological variates used as covariates, but the chlorophyll fluorescence measurements of T removed the effect of temperature (Figure 1) and reduced the harvest effect by 86% (Tables 2, 4). Consequently the T fluorescence measurement was judged the best covariate for explaining significant temperature and harvest effects. The O fluorescence measurement was considered to be the second best covariate (Tables 2, 4).

None of the covariates explained the differences among cultivars for tuber and total dry weights. The cultivars that had the highest total dry weight (Norchip, DTO-33, and Atlantic) had the highest leaf dry weight/stem dry weight ratio (Table 2). The typical effect of high temperature is to decrease the leaf/stem ratio (3, 13) and the results of this study

TABLE 2.—*Effect of cultivar, temperature and harvest on growth variates.*

Treatment	Tuber number plant^{-1}	Leaf dry wt.	Stem dry wt.	Root+stolon dry wt.	Tuber dry wt.	Total dry wt.
	($\sqrt{x}$)	---------- ($\log_{10}$ g plant^{-1}) ----------				
Cultivar (C)						
A14-0-11	1.49	−.203	−.864	−.264	−.728	0.441
Atlantic	1.48	−.100	−.906	−.334	−.504	0.487
Bintje	1.75	−.360	−.845	−.433	−.393	0.452
C14-343	2.24	−.332	−.939	−.598	0.202	0.444
Desiree	1.73	−.217	−.829	−.403	−.481	0.433
DTO-33	1.66	−.124	−.939	−.286	−.759	0.490
LT-1	1.51	−.252	−.891	−.368	−.432	0.417
Norchip	1.92	−.197	−1.024	−.595	0.023	0.503
Red Pontiac	1.57	−.264	−.899	−.376	−.434	0.448
Russet Burbank	1.05	−.143	−.746	−.268	−1.361	0.433
SEM (n=6 df=18)	0.112	0.0347	0.0191	0.0152	0.2699	0.0160
Temperature (T)						
20/15	2.25	−.218	−1.053	−.316	0.138	0.586
30/25	1.03	−.221	−.682	−.469	−1.111	0.323
SEM (n=30 df=18)	0.050	0.0155	0.0085	0.0068	.1207	0.0071
Harvest (H)						
1	1.12	−.380	−.964	−.365	−2.109	0.084
2	1.79	−.156	−.813	−.366	−.035	0.477
3	2.01	−.122	−.826	−.446	0.683	0.802
SEM (n=20 df=18)	0.061	0.0190	0.0105	0.0083	0.1478	0.0087
T × H						
20/15						
Harvest 1	1.92	−.352	−1.033	−.214	−.857	0.234
Harvest 2	2.24	−.195	−1.044	−.330	0.423	0.604
Harvest 3	2.58	−.107	−1.083	−.402	0.848	0.921
30/25						
Harvest 1	0.32	−.407	−.895	−.516	−3.360	−.065
Harvest 2	1.34	−.116	−.853	−.401	−.492	0.350
Harvest 3	1.44	−.138	−.568	−.491	0.519	0.684
SEM (n=10 df=18)	0.086	0.0269	0.0148	0.0118	0.2091	0.0124

suggest that selection for low leaf/stem dry weight ratio should result in clones that have high total dry weight. However, this does not necessarily translate into high tuber dry weight production because only one of the clones that had high total dry matter production (Norchip) also produced high tuber dry weight. Ben Khedher and Ewing (1) in a study of 11 different clones also identified Norchip as outstanding in its ability to tolerate high temperatures.

TABLE 3.—*Analysis of variance and covariance Mean Squares (MS) for tuber dry weight (log_{10} g plant^{-1}).*

Source of variation	df	ANOVA MS	Tuber dry weight MS adjusted for covariate: Leaf resp.	Leaf photo.	Leaf area	Chlorophyll fluorescence: O	P	T
Cultivar (C)	9	1.10*[1]	1.09*	1.04*	1.02*	1.07	0.88	1.17*
Temperature (T)	1	23.40**	13.32**	0.59[2]	4.83**	0.54	0.07	0.47
Harvest (H)	2	42.03**	13.42**	32.08**	7.06**	11.78**	37.40**	0.88
C×T	9	0.53	0.53	0.57	0.62	0.65	0.33	0.57
C×H	18	0.52	0.54	0.45	0.40	0.57	0.54	0.57
T×H	2	6.32**	3.86**	6.79**	6.43**	0.03	0.18	0.12
Covariate	(1)	—	0.36	1.07	1.07	1.09	1.54	0.90
Residual	18(17)	0.437	0.442	0.399	0.399	0.399	0.372	0.410

[1]P<0.05 and P<0.01 are denoted by * and **, respectively.
[2]Underlined MS values were significant before adjustment for covariate.

TABLE 4.—*Analysis of variance and covariance Mean Squares (MS) for total dry weight (log_{10} g plant^{-1}).*

Source of variation	df	ANOVA MS	Total dry weight MS adjusted for covariate: Leaf resp.	Leaf photo.	Leaf area	Chlorophyll fluorescence: O	P	T
Cultivar (C)	9	49*[1]	49*	36[2]	46*	44*	45*	35
Temperature (T)	1	10393**	7066**	1581**	3269**	82*	473**	25
Harvest (H)	2	25855**	9106**	13645**	9490**	13451**	25223**	3606**
C×T	9	28	27	28	32	23	27	28
C×H	18	14	14	14	14	14	14	14
T×H	2	49	36	38	56*	11	16	1
Covariate	(1)	—	0	11	62	7	3	0
Residual	18(17)	15.3	16.2	15.5	12.5	15.8	16.0	16.2

[1]P<0.05 and P<0.01 are denoted by * and **, respectively. The MS values have been multiplied by 10^4 for presentation in this table.
[2]Underlined MS values were significant before adjustment for covariate.

The significant changes in leaf dry weight due to harvest (Table 5) were removed when T fluorescence was used as a covariate, indicating the increase in leaf dry weight with harvest was associated with a decrease in T fluorescence (Table 1).

This survey confirmed the previously reported (2, 13) effect of high temperature increasing stem dry weight (Tables 2, 5). The greatest reductions in mean square values for stem dry weight (Table 5) were achieved

TABLE 5.—*Analysis of variance and adjusted Mean Squares (MS), using chlorophyll fluorescence T values as a covariate, for tuber number, and leaf, stem, and root and stolon dry weight. Dry weights are log_{10} g $plant^{-1}$.*

Source of variation	df	Tuber number		Leaf dry wt.		Stem dry wt.		Root + stolon dry wt.	
		MS	adj. MS	MS	adj. MS	MS	adj. MS	MS	adj. MS
Cultivar (C)	9	.59**	.62**[1]	437**	387**	447**	444**	885**	890**
Temperature (T)	1	22.22**	.08[2]	1	29	20690**	84	3553**	16
Harvest (H)	2	4.28**	.05	3914**	240	1405**	95*	439**	328**
C×T	9	.23*	.23*	88	73	197**	197**	426**	376**
C×H	18	.11	.13	82	83	49*	49	49**	51**
T×H	2	.64**	.32*	256	241	2078**	95*	832**	118**
Covariate	(1)	—	.29	—	28	—	2	—	52
Residual	18(17)	.075	.062	72.2	74.8	21.9	23.1	14.0	11.7

[1]P<0.05 and P<0.01 are denoted by * and **, respectively.
[2]Underlined MS values were significant before adjustment for T covariate.

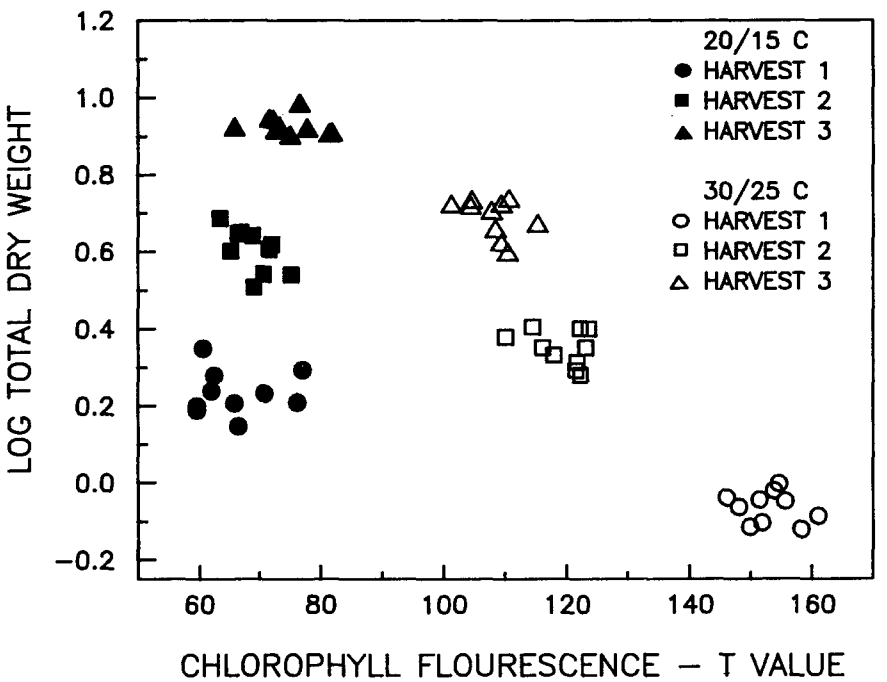

FIG. 1. Effect of cultivar, temperature and harvest on T chlorophyll fluorescence and total dry weight.

by using chlorophyll fluorescence parameters such as T as a covariate (Table 5), especially for the interaction between temperature and harvest.

Root and stolon dry weight was significantly affected by interactions amongst the three factors, cultivar, temperature and harvest (Tables 2, 5). Since the roots and stolons were not separated before weighing, it is not possible to determine if the roots and stolons responded differently. At 20/15°C the root and stolon weight was higher than at 30/25°C but the difference gradually declined over the growing season. At 30/25°C the root and stolon weight was lower but it did not change significantly over the growing season. Only the significant effect of temperature could be removed through the use of a covariate. Fluorescence parameters such as T were effective in removing this significant effect as well as considerably reducing the mean square value for the temperature × harvest interaction but not the effects for harvest and interactions with cultivars.

Leaf respiration, photosynthesis and area removed only parts of the factorial effects of temperature and harvest.

Tuber number, which can be used as a measure of tuber induction, was influenced mainly by an interaction between temperature and harvest and an interaction between cultivar and temperature (Tables 2, 5). Tuber numbers at the first harvest were much higher at 20/15°C than at 30/25°C. Tuber numbers increased with harvest date at both temperatures but the increase was slightly greater at 20/15°C. This result is in agreement with previous research that indicates temperatures greater than 20°C generally reduces tuber initiation (7). The covariate T fluorescence removed the effect of temperature and harvest and reduced the temperature × harvest interaction. The increase in tuber numbers with increasing photosynthetic rate and leaf area suggests that a reduction in tuber numbers under high temperature is probably due to a reduction in total photosynthate production in the haulm.

Conclusions

The results of this study confirm previous research (1, 2, 4, 13) indicating that high temperature increases dry matter partitioning to stems but reduces root, stolon, tuber and total dry matter and tuber number. In this study the high temperature decreased leaf area but not leaf dry weight, a response also reported by Ben Khedher and Ewing (1).

The analysis of covariance showed that the most effective covariate was the T chlorophyll fluorescence parameter. Since the increase in T was due to the increase in O, the most physiologically important covariate might be the O fluorescence parameter, but it was not as effective as T in the covariance analysis because of greater experimental error.

The covariance analyses indicated that the reduced dry weight production at high temperatures is not related to reduced leaf area reducing light

interception, or to increased maintenance dark respiration consuming photosynthates. The effectiveness of the O chlorophyll fluorescence parameter as a covariate clearly suggests that reduced efficiency in Photosystem II plays a major role in reduced potato growth at high temperatures.

The highest tuber yields were in clones that had high tuber numbers. Thus, it appears that the high temperature effect begins with a reduction in tuber initiation which reduces the demand for photosynthate translocation to tubers. High temperature may also reduce the ability of the plant to translocate photosynthate to tubers, which is indicated by the increase in stem dry weight at high temperatures in this study, producing a negative feedback on the photosynthetic system. Attempts have been made to alter translocation at high temperatures with paclobutrazol, an antigibberellin growth regulator that reduces the tendency to partition more dry matter to the stems at high temperatures (6). The paclobutrazol treatment reduced the partitioning to the stems but there was not a corresponding increase in the other plant components, suggesting that the problem is due to a reduction in tuber initiation and photosynthetic efficiency and not just poor translocation.

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