Photosynthesis at High Temperature in Tuber-Bearing *Solanum* Species[1]

A Comparison between Accessions of Contrasting Heat Tolerance

Matthew P. Reynolds[2], Elmer E. Ewing, and Thomas G. Owens*

Department of Vegetable Crops (M.P.R., E.E.E.) and Section of Plant Biology (T.G.O.) Cornell University, Ithaca, New York, 14853

ABSTRACT

Differences in the photosynthetic performance between pairs of heat tolerant (HT) and heat sensitive (HS) accessions of tuber-bearing *Solanum* species were measured at 40 °C, after treating plants at 40/30 °C. After 1 to 9 days of heat treatment, both HT and HS accessions showed progressive inhibitory effects, primarily decreased rates of CO_2 fixation, and loss of leaf chlorophyll. These effects were most pronounced in the HS accessions. Stomatal conductivity and internal CO_2 concentrations were lower for both accessions at 40 °C especially for the HS accessions, suggesting that at ambient CO_2 concentrations, stomatal conductance was limiting CO_2 availability at the higher temperature. In the HT accessions, stomatal limitations were largely attributed to differences in vapor pressure deficit between 25 ° and 40 °C, while the HS accessions exhibited significant nonstomatal limitations. The young expanding leaves of the HS accession showed some HT characteristics, while the oldest leaves showed severe senescence symptoms after 9 days at 40/30 °C. The data suggest that differences in heat sensitivity between HT and HS accessions are the result of accelerated senescence, chlorophyll loss, reduced stomatal conductance, and inhibition of dark reactions at high temperature.

It is one of the challenges of crop scientists to find ways of improving plant yield in stressful environments. One important approach to this work is to identify stress-related physiological processes that impair plant performance so that screening procedures can be developed to select better adapted cultivars. It is well established that whole leaf photosynthesis is inhibited at high temperatures in nonacclimated plants (1). However, for most crop species it is not known whether differences in the degree to which photosynthesis is impaired at elevated temperatures are causally related to differences in

plant performance. In potato (*Solanum tuberosum* L.) grown at high temperatures, tuberization is inhibited (8), elevated respiratory rates deplete photoassimilates (4), and photosynthetic carbon fixation declines at temperatures above 25 °C (6, 11). Nonetheless, there is considerable interest in growing potatoes in lowland tropical conditions (18) where air temperatures as high as 40 °C reduce yields (4, 7). The genetic potential for more heat tolerant photosynthesis in the many wild relatives of *S. tuberosum* has not been investigated systematically, although correlations between the thermal environments of several indigenous *Solanum* species and their Chl fluorescence induction under acute temperature stress have been reported (15).

In heat screening trials of 319 accessions of 59 tuber-bearing *Solanum* species, a wide range of responses to temperature were found among species and accessions (13). Using these data, pairs of HT[3] and HS accessions were chosen from four species that showed a range of heat tolerance among accessions. The contrast among accessions in their ability to produce shoot fresh weight during 4 weeks at 30 to 40 °C was a major factor in assigning their heat tolerance (Table I). After 4 weeks at 14 to 35 °C (controls), the shoot fresh weights were not significantly different between accessions, except in the case of *Solanum demissum* (Table I). At 30 to 40 °C, all accessions showed a decline in fresh weight compared with controls. However, fresh weights were 30% to 70% lower for the HS compared with the HT accessions at the higher temperature. The HS accessions also showed more of the following visual symptoms of high temperature stress: decreased leaf size, leaf rolling, more acute leaf angle to the stem, and senescence symptoms such as chlorosis and necrosis. In heat screening trials, photoperiods were long in both temperature regimes to prevent the complicating effects of tuberization on shoot growth (3). Prolific canopy growth is a prerequisite to good tuber yield (19); tuberization characteristics were assessed after selection for shoot growth (13).

In the present study, photosynthetic performance at elevated temperature was examined in four pairs (one HT and one HS) of accessions selected on the basis of our previous screening study (13). Plants were acclimated to 40/30 °C in

[3] Abbreviations: HT, heat tolerant; HS, heat sensitive; VPD, vapor pressure deficit.

Table I. *Fresh Weights of Pairs (HT and HS) of 10-wk-Old Accessions of Four Solanum Species after 4 wk at 30 to 40°C or 14 to 35°C in Greenhouses*

Values are means of 3 years of screening data adapted from Table II in Reynolds and Ewing (13).

Species	Fresh Weight of Accession[a]	
	14 to 35°C	30 to 40°C
	g/plant	
S. bulbocastaunum		
HT	24	17
HS	16	10*
S. chacoense		
HT	33	32
HS	32	13*
S. demissum		
HT	34	23
HS	17*	5*
S. stoloniferum		
HT	21	12
HS	25	6*

[a] An asterisk denotes a statistically significant (P < 0.05) difference between a pair of accessions within the same temperature treatment.

growth chambers for up to 9 d, when stress symptoms of plants were comparable to those seen on plants after 3 weeks or more of screening at 30 to 40 °C in the greenhouse. Even before stress symptoms became visible, photosynthetic rates at 40 °C were lower for the HS accessions than the HT ones. Our results suggest that Chl loss, reduced stomatal conductivity and accelerated senescence were the major factors accounting for the difference in photosynthetic performance between HT and HS accessions at high temperature.

MATERIALS AND METHODS

Growing Conditions

The following accessions selected for heat tolerance or sensitivity in the previous study (13) were used: *Solanum chacoense* (PI 209411, PI 275141), *Solanum demissum* (PI 338618, PI 160230), *Solanum stoloniferum* (PI 255532, PI 160224), and *Solanum bulbocastaunum* (PI 347757, PI 275195). The first accession listed in each pair was tolerant, the second was sensitive. Accession numbers are those of the Plant Introduction Station, Sturgeon Bay, WI, from which the seeds were obtained. Plants were raised from seed (not tubers) in greenhouses at 20 to 30 °C, in 14 cm plastic pots. Six to 9 week old plants were transferred to growth chambers 1 week before each experiment began. The photon flux density in the chambers at unshaded soil level was 350 μmol m^{-2} s^{-1} PAR (about 500 μmol photons m^{-2} s^{-1} at the surface of an average leaf used for photosynthesis measurements), and the day/night temperature regime was 25/20 °C with a 14 h photoperiod. Photosynthesis was measured on plants that had not tuberized so as to be comparable to the screening study. Control rates of photosynthesis were measured at 25 °C prior to heat treatment. Rates were later measured at 40 °C on the same plants after 1 to 9 d of heat treatment at 40/30 °C day/

night regime. From 3 to 12 leaf samples were measured for each treatment, with leaves being selected from three to six plants per accession.

O₂ Evolution

Oxygen evolution was measured on fresh leaf discs (3 cm^2) at saturating CO_2 and humidity using a Hansatech LD-2 electrode (5). Discs were cut from the center of mature healthy leaves that were located at least six nodes below node 1, unless otherwise stated. Node 1 was defined as the node bearing the youngest leaf that had an area greater than 5 cm^2. Full leaf expansion occurred below approximately the sixth node. Illumination was provided by a quartz-halogen source that was filtered to remove IR. Light intensity was varied by using neutral density filters. Discs from control and heat-treated plants were measured at 25 and 40 °C, respectively. Rates of oxygen evolution were normalized to the total Chl $a + b$ content of each leaf disc.

Chl

Chl a and b were measured immediately after rates of oxygen evolution had been recorded, on the same leaf discs. Pigments were rapidly extracted in 90% acetone, and spectrophotometric readings were quantified using the equations of Jeffrey and Humphrey (9).

Gas Exchange

Carbon fixation was measured with a null-balance steady state gas exchange system (PACsys 9900, Data Design Group, CA). All measurements were made on attached mature leaves at a CO_2 concentration of 330 μL/L, a relative humidity of 50%, and at a photon flux density of 450 μmol m^{-2} s^{-1} (PAR) from a sodium discharge lamp. Leaf temperature was determined by a thermocouple in direct contact with the leaf surface and was set to either 25 °C (control) or 40 °C (heat-treated). In all cases, air temperature varied by less than 2 °C from the set leaf temperature. Leaves were chosen by the same criteria described under O₂ evolution. The same leaves were used for control measurements at 25 °C and for measurements at 40 °C after heat treatment.

RESULTS

Oxygen Evolution

Oxygen evolution was measured as a function of light intensity in *S. chacoense* control plants and plants which had been heat treated at 40/30 °C for 2 d (Fig. 1). Both accessions behaved very similarly in response to light intensity at 25 °C, and only the data for the HS accession are presented in Figure 1. No significant differences between the HT and HS accessions at 25 °C or 40 °C were detectable at light limiting intensities (<300 μmol photons m^{-2} s^{-1}). However, marked differences were observed at light intensities approaching saturation (>500 μmol photons m^{-2} s^{-1}). At 40 °C, the HT accession reached the same light-saturated rate of O₂ evolution as the controls but had higher rates than control plants between 500
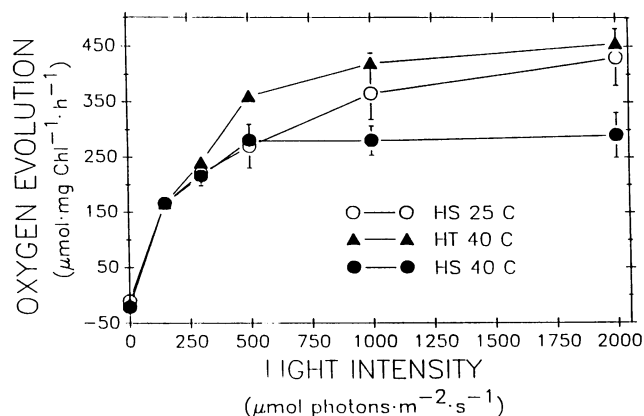
Figure 1. Light intensity dependence of the rate of O_2 evolution in leaf disks (measured at saturating CO_2 and humidity) at 40 °C, after 2 d of heat treatment of 40/30 °C, and at 25 °C prior to heat treatment, for HT and HS accessions of *S. chacoense*. Vertical bars represent standard errors of the means of four replications. At 25 °C, the response of the HT accession to light intensity was not significantly different from that of the HS accession.

and 1000 μmol photons m^{-2} s^{-1}. In contrast, the HS accession showed lower rates at all intensities above 500 μmol photons m^{-2} s^{-1} (Fig. 1). In all cases, a light intensity of 2000 μmol photons m^{-2} s^{-1} was adequate to saturate rates of O_2 evolution without any apparent photoinhibition.

Variations in the rate of O_2 evolution measured at 500 μmol photons m^{-2} s^{-1} during nine days of 40 °C heat treatment are shown in Figure 2 for *S. chacoense*. Similar patterns were observed in the other three pairs of accessions. An intensity of 500 μmol photons m^{-2} s^{-1} was selected for measurement of O_2 evolution because it was within the range experienced by leaves in growth chambers and under screening conditions in greenhouses (13), and is also the intensity where HT and HS plants showed the greatest difference in rate (Fig. 1). The HT accession exhibited a significant increase in rate at d 3 while there was no significant change in the HS rate (Fig. 2). After d 3, the HT and HS accessions showed parallel declines in O_2 evolution with the HS rates about 20% less than those of the HT accession. Rates measured on nonacclimated plants under acute stress conditions (10 min at 40 °C) were not significantly different between accessions (Fig. 2), and not significantly different from control rates measured at 25 °C (Fig. 1). In limiting light (<300 μmol photons m^{-2} s^{-1}), rates of O_2 evolution did not show a significant decline in any accession prior to d 5. However, after d 5 the HS accessions exhibited a significant decrease in rates at limiting light intensities while the rates of the HT accessions were the same as controls (not shown).

Maximal rates of O_2 evolution measured at 40 °C, after 1 to 3 d of heat treatment at 40/30 C, averaged 45% lower for the HS accession of *S. chacoense* and 10 to 17% lower for the other species (Fig. 3) compared to their respective HT accessions. An experiment conducted with plants acclimated for 4 d to greenhouse conditions identical to those used to screen plants for high temperature (30–40 °C, and 18-h photoperiod)

(13) showed the same trends for the species *S. chacoense, S. stoloniferum,* and *S. bulbocastaunum*: that is, HT accessions showed higher maximal rates of O_2 evolution than HS accessions at 40 °C (not shown).

During the course of our studies, we frequently observed that younger leaves of the HS accession exhibited less pronounced effects of heat treatment than did mature, fully expanded leaves on the same plant. To investigate the effect of leaf age on heat tolerance, light saturated rates of O_2 evolution were measured on expanding leaves, which were generally located above the sixth node from the top of the plant. In contrast to the mature leaves, differences in the young expanding leaves were not detected between accessions of *S. chacoense* (Fig. 4), or *S. stoloniferum* (not shown) after 1 to 3 d heat treatment at 40/30 °C. The rates of O_2 evolution in these younger HS leaves were equal to the rates found in the mature leaves of the tolerant accession. Furthermore, the Chl *a* to Chl *b* ratio and Chl content per cm^2 leaf area were not significantly different between the young and mature leaves. In a separate experiment, there was no apparent effect of leaf age on light-saturated O_2 evolution in control plants (25 °C) of either accession.

Gas Exchange

After 2 to 3 d of heat treatment at 40/30 °C, carbon fixation rates per leaf area, measured at 40 °C and 50% RH, were 45% lower for the HS accessions of *S. chacoense* than for the tolerant accession (Table II). There was a similar but smaller difference (27%) between the HT and HS accessions of *S. stoloniferum* (Table II). Stomatal conductances at 40 °C (Table II) were lower in the HS than in the HT accessions of both species. All accessions showed lower stomatal conductances at 40 °C than for controls at 25 °C (Table II). The internal CO_2 data were variable but seemed to be lower for HS accessions at 40 °C, and lower for all accessions at 40 °C in comparison to controls at 25 °C (Table II). The values of stomatal conductance and internal CO_2 concentration were
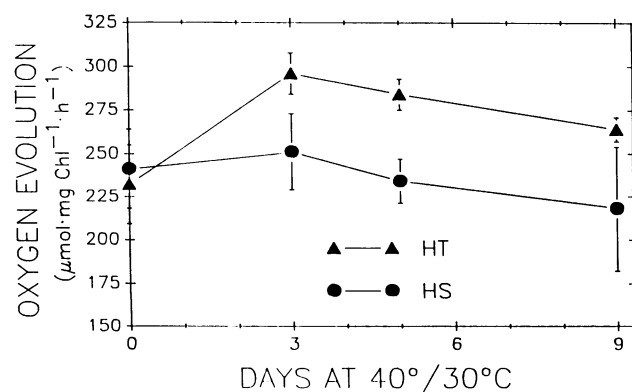

Figure 2. Rates of O_2 evolution from leaf discs (measured at saturating CO_2 and humidity) at 40 °C and a light intensity of 500 μmol photons m^{-2} s^{-1}, prior to heat treatment and after 3, 5, and 9 d at 40/30 °C, for HT and HS accessions of *S. chacoense*. Vertical bars represent the standard error of the means of four to eight replications.
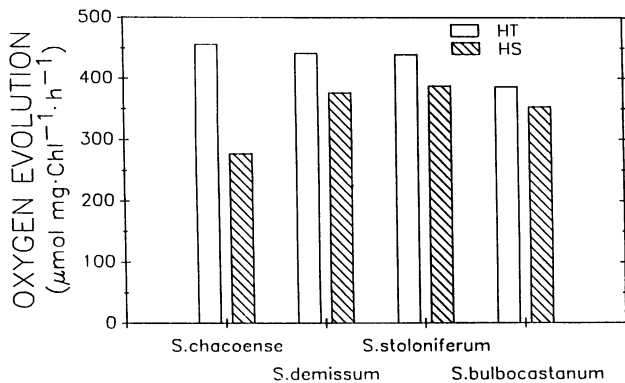
Figure 3. Light-saturated rates of O_2 evolution from leaf disks (measured at saturating CO_2 and humidity) at 40 °C after 1 to 3 d of heat treatment at 40/30 °C, for HT and HS accessions of four *Solanum* species. The difference between HT and HS accessions were significant at the 5% level or greater, except for *S. bulbocastaunum* which was significant at the 14% level. Values represent means of eight replications.

not significantly different after 5 d at 40/30 °C in *S. chacoense* from those recorded after 2 to 3 d heat treatment for either accession. During the same period of treatment, the rate of CO_2 fixation remained constant for the HT accession but declined by 60% in the sensitive plants. Beyond d 5, declines in CO_2 fixation rates at 40 °C generally paralleled the loss of leaf Chl (see below). At 25 °C and 50% RH, there were no apparent differences between accessions in any of the variables measured, but values were generally higher than those at 40 °C for either accession (Table II).

In order to evaluate the direct effect of VPD on stomatal conductance and CO_2 fixation between control and heat treated plants, experiments with *S. chacoense* were repeated with the RH of the leaf chamber was adjusted to 30% at 25 °C and to 70% at 40 °C so that the VPD from air to leaf was comparable between temperature treatments. In both accessions, this reduced the differences in stomatal conductance between 25 and 40 °C. Under these conditions, the rate of CO_2 fixation for the HT accession at 40 °C was comparable to both accessions at 25 °C and had a value of 13.5 μmol CO_2 m^{-2} s^{-1}. In contrast, the HS accession had a rate of 9.0 μmol CO_2 m^{-2} s^{-1}, showing a 33% inhibition at 40 °C compared to the other treatments.

Chl

Changes in leaf Chl content and Chl a to Chl b ratios also contributed significantly to the decline of photosynthetic performance in *S. chacoense* during 9 d of heat treatment at 40/30 °C (Fig. 5). In the HS accession, leaf Chl content declined slightly during the first 3 d of treatment and subsequently fell by more than 50% after 9 d. Over the same period, the Chl a to Chl b ratio increased from 4.5 to 7.7. In contrast, the leaf Chl content of the HT accession dropped by only 14% after 9 d at 40/30 °C without significant changes in the Chl a to Chl b ratio.

DISCUSSION

The four pairs of HT and HS accessions used in our experiments were chosen from a previous screening of 59 species (13). In some of the species not selected for the present study, all accessions died within a few days of exposure to high temperatures, while in still other species all accessions grew into healthy plants under heat stress. In general, the HS accessions selected for the present study responded to high temperatures by showing progressive senescence symptoms and reduced growth rates over the 4 weeks of screening. During the same period, the HT accessions showed significant shoot growth and fewer stress symptoms. By comparing related accessions within the same species, we hoped to determine whether differences in photosynthesis could account for the widely varying responses of shoot growth to high temperature.

The apparent heat tolerance of young leaves in HS accessions, as evidenced by their light saturated rates of O_2 evolution (Fig. 4), suggests that heat sensitivity may to some extent be a manifestation of accelerated senescence. Though not fully expanded, leaves between nodes 1 and 6 exhibited identical rates of light-saturated O_2 evolution at 25 °C (per cm^2 leaf area and per Chl), total Chl $a + b$ per cm^2 leaf area, and Chl a to Chl b ratios, suggesting that these leaves are photosynthetically competent. Leaves of *S. tuberosum* show loss of photosynthetic capacity with age (20), which is accelerated by high temperature (4). Although the young leaves of HS accessions showed characteristics of heat tolerance, we estimated that they accounted for less than one third of the plant's total leaf area.

A progression of effects was observed in *S. chacoense* as plants responded to 40/30 °C over the 9-d study period. Although no accessions showed visible manifestations of stress during the first 4 d of heat treatment, there were clear differences between accessions in photosynthetic performance.
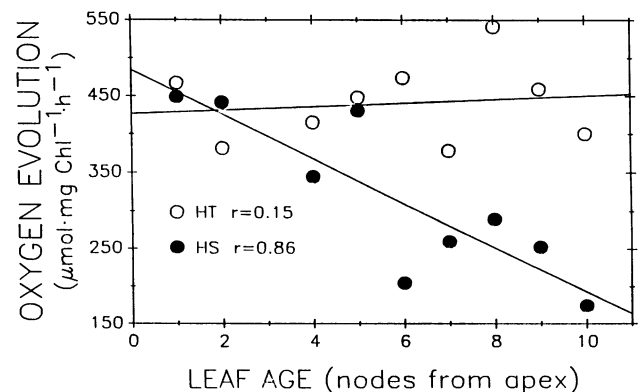

Figure 4. Effect of leaf age on the light saturated rate O_2 evolution from leaf disks (measured at saturating CO_2 and humidity) at 40 °C, for HT and HS accessions of *S. chacoense* after 1 to 3 d of heat treatment at 40/30 °C. The Spearman correlation coefficient of rate of O_2 evolution on leaf age had a P value of 0.003 for the HS accession and was not significant for the HT accession. Each data point represents a mean of two to four replications.

Table II. *Net Photosynthesis, Stomatal Conductance, and Internal CO_2 Concentration of Intact Leaves of HT and HS Accessions of S. Chacoense and S. Stoloniferum at 25°C, and at 40°C after 2 to 3 d at 40/30°C.*

For *S. chacoense* the protected LSD (PLSD) is given for comparisons between treatment means.

Species	Net Photosynthesis	Stomatal Conductance	Internal [CO_2]
	$\mu mol \; CO_2 \; m^{-2} \; s^{-1}$	$mm \; s^{-1}$	$\mu L \; L^{-1}$
S. chacoense			
25°C HT	14.4[a]	2.4	180
25°C HS	14.6	2.1	160
40°C HT	10.3	0.9	51[b]
40°C HS	5.7	0.4	25[b]
PLSD	1.8	0.4	35
S. stoloniferum			
25°C HT	14.7 (0.3)	3.2 (0.8)	205 (29)
25°C HS	17.3 (0.3)	3.0 (0.5)	184 (23)
40°C HT	16.0 (0.4)	1.9 (0.1)	120 (10)
40°C HS	11.5 (1.6)	0.5 (0.2)	18 (18)[b]

[a] Values represent means of 12 replications. For *S. stoloniferum* the standard error is given in parentheses after each mean, as replications (three to six) were not always equal between treatments. [b] Calculated values of internal CO_2 concentration were in some cases near or below expected compensation points, probably because of lack of sensitivity of the gas exchange system to small fluxes of gases at relatively low rates of CO_2 fixation.

After 2 d at 40 °C, CO_2-saturated rates of O_2 evolution were significantly lower for HS accessions in comparison to HT accessions at light intensities above 300 μmol photons m^{-2} s^{-1}. Rates of CO_2 fixation measured at 550 μmol photons m^{-2} s^{-1} were also inhibited in HS accessions in comparison with HT accessions. After 4 to 5 d at 40/30 °C, visible stress symptoms started to appear in HS accessions, and leaf Chl content began to drop. At the same time, there was a coincident decline in Chl *a* to Chl *b* ratios and in rates of light-limited O_2 evolution (in addition to a continued difference in light-saturated rates). A further decrease in rates of CO_2 fixation per cm^2 leaf area for the HS accession between 5 and 9 d paralleled the loss of total leaf Chl. By the end of 9 d in the hot growth chamber, HS accessions exhibited visible stress symptoms equivalent to those observed after 3 weeks or more of heat screening in the greenhouse (13).

In general, the rate of photosynthesis is expected to rise with increasing temperature as a result of the Q_{10} effect (increase in reaction rate accompanying a 10 °C temperature increase) (1). We observed in *S. chacoense* that the maximal rates of O_2 evolution at 40 °C after 1 to 3 d heat treatment were lower for the HS accession in comparison to rates for control plants at 25 °C, while rates were comparable or only slightly increased in the HT accession (Fig. 1). Similarly, the rates at 500 μmol photons m^{-2} s^{-1} measured after acute temperature stress (40 °C for 10 min) were only slightly higher than the control rates (25 °C) for both HT and HS accessions of *S. chacoense* (Figs. 1 and 2). The fact that increased rates were not observed at 40 °C indicates that key reactions of

photosynthesis were inhibited in both HT and HS accessions. However, this inhibition was clearly more pronounced in the HS accessions of all four species. Although Chl loss was a major contribution to decreases in leaf photosynthesis (per leaf area), measurements normalized to Chl also indicate effects that are independent of leaf Chl content (Fig. 2).

Metabolic adaptation may have contributed to the superior performance of the HT accession after heat treatment at 40/30 °C. Evidence for this comes from the fact that rates of O_2 evolution (measured near ambient light at 500 μmol photons m^{-2} s^{-1}) at 40 °C were higher after heat treatment at 40/30 °C than the rates measured after acute exposure to temperature stress (Fig. 2). In bean, acquired heat tolerance has been shown to accompany changes in thylakoid lipid composition after a few days exposure to high temperature (17).

At 500 μmol photons m^{-2} s^{-1}, rates of O_2 evolution in saturating CO_2 were the same or higher for both accessions at 40 °C compared to 25 °C controls (Fig. 1). In contrast, rates of CO_2 fixation at ambient CO_2 were inhibited in both accessions at 40 °C (Table II). These data suggest that CO_2 availability, rather than the capacity for electron transport (16) or Calvin cycle turnover, appeared to be the major factor directly determining the difference in photosynthesis between HT and HS accessions at 40 °C. This hypothesis is also supported by the observation that rates of electron transport, calculated from CO_2 fixation at ambient CO_2 (Table II), were approximately a factor of 2 lower than rates calculated from O_2 evolution at saturating CO_2 (Fig. 2) for all treatments. The lower values for stomatal conductivity and internal CO_2 at 40 °C in comparison to 25 °C (Table II) also suggest that differences in the stomatal response between HT and HS accessions accounted for the differences in CO_2 fixation rates. The HS accessions were also observed to require less water in the growth chambers at 40/30 °C.

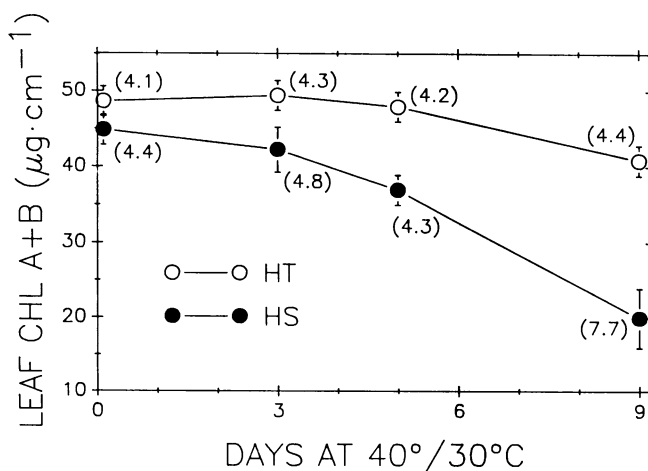It is well established that high VPD, which is likely to occur

Figure 5. Leaf Chl *a* + *b* content prior to heat treatment and after 3, 5, and 9 d at 40/30 °C for HT and HS accessions of *S. chacoense*. Vertical bars represent the standard errors of the means of four to eight replications. The ratios of Chl *a* to Chl *b* are shown next to the standard error bars.

REYNOLDS *ET AL.*

at elevated temperature, can reduce stomatal conductance, although there are also reports of a loss of sensitivity of stomatal movement at high temperature (21). When relative humidities were adjusted to maintain a similar VPD at 25 °C and 40 °C, the rates of CO_2 fixation were the same for the HT accession of *S. chacoense* at both temperatures, indicating that increased VPD may be a primary factor in reduced CO_2 fixation at 40 °C for the HT accession. Inhibition of photosynthesis due to high vapor pressure deficits at elevated temperature has also been reported in ryegrass (23). In the HS accession, even after correction for VPD differences, the rate of CO_2 fixation at 40 °C was more than 30% lower than the HT accession, indicating that factors other than stomatal conductance were contributing to depressed photosynthesis in the HS accession. Several studies have demonstrated inhibition of Calvin cycle activity resulting from inactivation of ribulose-1,5-bisphosphate carboxylase/oxygenase at high temperature (10, 22) that could account for the VPD-insensitive inhibition of CO_2 fixation we observe. However, the conclusion that stomatal factors contribute to decreased photosynthesis at elevated temperature is contrary to previous work in potato (6) and other species (1, 12, 14). If stomatal limitations are present, an obvious consequence of reduced internal CO_2 concentration at high temperature would be an increase in the rate of photorespiration, especially as the compensation point of ribulose-1,5-bisphosphate carboxylase/oxygenase has been shown to increase with temperature (24).

Chl loss, which was significant in *S. chacoense* after 5 d at 40/30 °C (Fig. 5), undoubtedly had a major impact on biomass accumulation. Loss of total Chl $a + b$ probably accounts for most of the decreased CO_2 fixation observed after d 5 (Fig. 5). However, the species *S. stoloniferum* did not show the same propensity for Chl loss after 10 d in the growth chamber 40/30 °C (not shown). Visual observations of 319 accessions of 59 *Solanum* species screened for heat tolerance (13) indicated considerable variation in the degree of chlorosis developing as a stress response at high temperature. The choice of chlorosis alone as a screening criterion would not be an effective way of removing all of the HS genotypes from a population of wild potato species.

After 5 d or more at 40/30 °C, differences in rates of O_2 evolution between HT and HS accessions were detectable at both saturating and limiting light intensities. The latter suggests a decrease in the quantum yield of photosynthesis which could result from a decrease in functional light-harvesting antenna size. The decline in total Chl $a + b$ per cm² leaf area and a preferential loss of Chl b in the HS accession supports a heat-induced loss of light-harvesting complexes. In addition, decreased quantum yield would also result from heat-induced dissociation of PSII light-harvesting complexes (2).

Comparison of the results between the 4-week screening study (13) and the measured photosynthetic parameters of the present study were not direct. For example, the CO_2 fixation rates for HT accessions at 40 °C relative to the control rates (Table II) indicated an inhibition for *S. chacoense*, but there was no difference between temperature treatments for *S. stoloniferum* (Table II). The difference was not reflected by the response of their shoot weights to high temperature (Table I). This may be due in part to the differences of temperature

and light environment between the screening treatments and the conditions under which photosynthetic parameters were measured. The temperature optimum for each accession is unknown, so a true control was not possible; it therefore seemed reasonable to measure photosynthesis at temperatures representing both ends of the day time temperature range at which plants were screened (13) in order to establish the potential differences in photosynthesis.

These data establish that photosynthetic response to high temperature can vary significantly within a species. A causal link between decreases in photosynthetic performance and and shoot growth at high temperature is inferred most strongly by the Chl loss seen in the HS accession of *S. chacoense,* and by the reduced CO_2 fixation rates seen in the HS accessions of *S. chacoense* and *S. stoloniferum,* in comparison to their respective HT accessions. The kinds of measurements described in this paper are time consuming and clearly not suitable to screening germplasm for photosynthetic characteristics on a large scale. Nonetheless they help to establish mechanisms that contribute to reduced plant performance at high temperature.

LITERATURE CITED

1. **Berry JA, Bjorkman O** (1980) Photosynthetic response and adaptation to temperature in higher plants. Annu Rev Plant Physiol **31**: 491–453
2. **Bilger W, Schreiber U, Lange O** (1984) Determination of heat resistance: Comparative investigations of chlorophyll fluorescence changes and tissue necrosis methods. Oecologia **63**: 256–262
3. **Bodleander KBA** (1963) Influence of temperature radiation and photoperiod on development and yield. *In* JD Ivins, EL Milthorpe, eds, The Growth of the Potato. Butterworths, London, pp 199–210
4. **Burton WG** (1972) The response of potato plant and tuber to temperature. *In* AR Rees, KE Cockshull, DW Hand, RG Hurd, eds, Crop Processes in Controlled Environments. Academic Press, New York, pp 217–233
5. **Delieu T, Walker DA** (1981) Polarographic measurement of photosynthetic O_2 evolution by leaf disks. New Phytol **89**: 165–178
6. **Dwelle RB, Kleinkopf GE, Pavek JJ** (1981) Stomatal conductance and gross photosynthesis of potato (*Solanum tuberosum* L.) as influenced by irradiance, temperature and growth stage. Potato Res **24**: 49–59
7. **Ewing EE, Keller ER** (1983) Limiting factors to the extension of the potato into non-traditional climates. *In* WJ Hooker, ed, Proceedings of the International Congress in Celebration of the Tenth Anniversary of the International Potato Center. International Potato Center, Lima, pp 22–27
8. **Gregory LE** (1956) Some factors for tuberization in potato plants. Am J Bot **43**: 281–288
9. **Jeffery SW, Humphrey GF** (1975) New spectrophotometric equations for determining chlorophylls a,b,c_1 and c_2 in algae phytoplankton and higher plants. Biochem Physiol Pflanzen **167**: 191–194
10. **Kobza J, Edwards GE** (1987) Influence of leaf temperature on photosynthetic carbon metabolism in wheat. Plant Physiol **83**: 69–74
11. **Ku G, Edwards E, Tanner CB** (1977) Effects of light, carbon dioxide, and temperature on photosynthesis, oxygen inhibition of photosynthesis and transpiration in *Solanum tuberosum.* Plant Physiol **59**: 868–872
12. **Raschke K** (1970) Temperature dependence of CO_2 assimilation and stomatal aperture in leaf sections of *Zea mays.* Planta **91**: 336–363

13. **Reynolds MP, Ewing EE** (1989) Heat tolerance in tuber-bearing *Solanum* species: a protocol for screening. Am Potato J **66**: 63–74

14. **Seemann JR, Berry JA, Downton WJS** (1984) Photosynthetic response and adaptation to high temperature in desert plants. A comparison of gas exchange and fluorescence methods for studies of thermal tolerance. Plant Physiol **75**: 364–368

15. **Smillie RM, Hetherington SE, Ochoa O, Malagamba P** (1983) Tolerances of wild potato species from different altitudes to cold and heat. Planta **149**: 112–118

16. **Stitt M** (1986) Limitations of carbon metabolism. I. Evidence for excess electron transport capacity in leaves carrying out photosynthesis in saturating light and CO_2. Plant Physiol **81**: 1114–1122

17. **Suss K-H, Yordanov IT** (1986) Biosynthetic cause of *in vivo* acquired thermotolerance of photosynthetic light reactions and metabolic responses of chloroplasts to heat stress. Plant Physiol **81**: 192–99

18. **Swaminathan MS, Sawyer RL** (1983) The potential of potato as a world food. *In* WJ Hooker, ed, Proceedings of the Interna-tional Congress in Celebration of the Tenth Anniversary of the International Potato Center. International Potato Center, Lima, pp 3–4

19. **Van der Plank JE** (1947) Some climatic factors determining high yields of potatoes. II. The potato at low altitudes and high altitudes. J Exper Agric **14**: 1–8

20. **Vos J, Oyarzun PJ** (1987) Photosynthesis and stomatal con-ductance of potato leaves—effects of leaf age, irradiance, and leaf water potential. Photosynth Res **11**: 253–264

21. **Vosch R, Tenhunen JD** (1981) Stomatal responses to humidity. *In* PG Jarvis, TA Mansfield, eds, Stomatal Physiology. Cam-bridge University Press, Cambridge, pp 137–161

22. **Weis E** (1981) Reversible heat-inactivation of the Calvin cycle: a possible mechanism of the temperature regulation of photo-synthesis. Planta **141**: 33–39

23. **Woledge J, Parsons AJ** (1986) The effects of temperature on the photosynthesis of ryegrass canopies. Ann Bot **57**: 487–497

24. **Wolf S, Olesinski AA, Rudich J, Marani A** (1990) Effects of high temperature on photosynthesis in potatoes. Am J Bot **65**: 179–189