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Effect of light on photosynthetic capacity during cold acclimation in a cold-sensitive and a cold-tolerant potato species

Kenneth L. Steffen and Jiwan P. Palta

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The effect of low temperature acclimation at various light levels on the photosynthetic capacity of *Solanum* species was examined. Two species, *Solanum tuberosum* L. cv. Red Pontiac and *Solanum acaule* Bitt., which differ significantly in degree of frost-tolerance and in their ability to acclimate to low temperature stress, were compared. Acclimation conditions included 5/2°C (day/night) temperatures and either moderate (400 $\mu mol \cdot m^{-2} \cdot s^{-1}$) or low (40 $\mu mol \cdot m^{-2} \cdot s^{-1}$) photosynthetic photon flux densities. Several parameters of photosynthesis were measured in tissue pieces during acclimation treatments including chlorophyll content, chlorophyll *a*/*b* ratios and carbon dioxide-saturated photosynthetic oxygen evolution during light-limited and light-saturated assays.

Most measured photosynthetic parameters of low temperature-grown plants of both species showed greater declines under the moderate light than the low light conditions. Chlorophyll *a*/*b* ratios were unchanged after low temperature exposures in both light level treatments. At low temperatures, the cold-sensitive *S. tuberosum* demonstrated a greater inhibition of photosynthetic capacity in light- and carbon dioxide-saturated assays than *S. acaule* at all light levels. In addition to a pronounced inhibition at the higher light level, *S. tuberosum* demonstrated a very strong inhibition of photosynthetic capacity at very low light levels. Our results suggest a correlation between ability to maintain essential metabolic processes during low temperature stress in the presence of moderate light levels and the ability to increase cold tolerance.

Additional key words – Chlorophyll, frost tolerance, low temperature, photoinhibition, respiration, *Solanum acaule, Solanum tuberosum.*

K. L. Steffen and J. P. Palta (reprint requests), Dept of Horticulture, Univ. of Wisconsin, Madison, WI 53706, USA.

Introduction

Considerable variation in response to low temperature exists among tuber-bearing *Solanum* species (Li 1977, Estrada 1978, Palta and Li 1979, Li et al. 1981). The inability of some species, including the cultivated *Solanum tuberosum,* to increase their frost hardiness after several weeks of exposure to low, non-freezing temperatures is in marked contrast to some of the closely-related wild species which are able to lower their frost-killing temperature by as much as 7.5°C (Li et al. 1981).

The acclimation of *Solanum* species to low temperature appears to be a metabolically active phenomenon involving the accumulation of increased levels of cellular protein, carbohydrates and lipids (Chen and Li 1980). In *Brassica napus,* acclimation has also been shown to be correlated with increased ATP levels (Sobczyk et al. 1985). Metabolic energy and fixed carbon necessary to support the relatively long-term acclimation process must come ultimately from photosynthesis (Kacperska-Palacz 1978, Gusta and Fowler 1979), one of the plant functions most sensitive to environmental stress.

Numerous studies have documented the light-dependent decline of photosynthetic capacity (photoinhibition) upon exposure to low temperature stress, how-

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ever, much of this work has been done with chilling-sensitive plants or cold-hardy tree species (see for reviews Öquist 1983 and Powles 1984). The effect of light on photosynthesis during long-term, low temperature exposure of cold-tolerant herbaceous plants has received little attention. In one early study, spinach, a chilling-resistant plant, demonstrated no apparent photoinhibition in leaf discs exposed for 40 h to low temperature at either high or low light levels (Garber 1977). In contrast, a recent study by Ögren et al. (1984) has shown that *Lemna gibba,* a chilling-resistant aquatic plant, exhibits substantial photoinhibition at low, non-freezing temperatures during short-term exposures at low to moderate light levels. While the potato is generally considered to be chilling-resistant, symptoms of injury such as yellowing (Palta and Jensen 1981) and necrosis (K. L. Steffen and J. P. Palta, unpublished results), occurring differentially among potato species, have been observed during growth at low, non-freezing temperatures.

To our knowledge comparative studies on the effect of light level and low temperature on the photosynthetic capacity of chilling-resistant herbaceous plants has not been reported. Furthermore, comparative studies of genetically related material have not been attempted. The purpose of the present investigation was to determine the effect of light level on the photosynthetic capacity of potato plants maintained for several weeks at low temperatures. *Solanum* species which vary in their cold-tolerance, were compared in order to test for a possible relationship between the ability to maintain photosynthesis during low temperature stress and the ability to frost-acclimate. A portion of this study was presented at the Annual Meeting of the American Society of Plant Physiology (Steffen and Palta 1984).

Materials and methods

Plant material and growth conditions

Two tuber-bearing *Solanum* species were used in this study; *S. tuberosum* L. cv. Red Pontiac, a cold-sensitive species which is frost-killed at −2.5°C and cannot further acclimate at low temperatures and a cold-hardy *S. acaule* Bitt. which is frost-killed at −6.0°C before, and at −9.0°C after, acclimation. Clonal material was started as propagules in tissue culture on MS media (Murashige and Skoog 1962) and stem sections from this material were rooted in peat plugs with 100% relative humidity for 10 days. Rooted plantlets were transferred to 15 cm diameter pots filled with 1:1 (w/w) milled sphagnum and perlite (Jiffy Mix, JPA, West Chicago, IL, USA) and grown for two months at 20/15°C (light/dark) with 14 h of 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux densities (400–700 nm) from cool white fluorescent and incandescent lamps (Sylvania/GTE, Danvers, MA, USA). Throughout the studies the plants were irrigated four times daily with one-half strength Hoagland's nutrient solution (Hoagland and Arnon 1950), supplemented with an additional 2.5 m*M* $Ca(NO_3)_2$. The nutrient solution was supplied in excess to prevent salt build-up. At time zero of the treatments, pots containing two-month-old plants were transferred into black cloth compartments, with open or screened tops, to provide either 400 or 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ average irradiances, at the top of the plant canopy and perpendicular to the light bank, hereafter referred to as moderate and low light, respectively. Plants from these light levels were subdivided for analysis into a total of 4 light levels on the basis of actual incident light levels at the leaflet surface. Temperatures were maintained at 5/2°C in walk-in growth rooms at the Univ. of Wisconsin Biotron.

Photosynthetic oxygen evolution and respiratory oxygen uptake

Using a technique similar to that of Ishi et al. (1977), photosynthetic oxygen evolution and respiratory oxygen uptake were determined using a Clark-type oxygen electrode (Model 53, Yellow Springs Instruments, Yellow Springs, OH, USA). Prior to excision of leaf tissue for use in assays, actual incident light levels perpendicular to the surface of the leaflets were measured with a Li-600 quantum meter (Li-Cor Inc., Lincoln, NE, USA). Terminal leaflets were excised from the third to fifth leaf node (*S. tuberosum*) and the sixth to eighth leaf node (*S. acaule*). These were the youngest 'fully expanded' leaves in these species. Four leaf discs (0.65 cm diameter) were cut from the leaflets, then sliced into pieces about 1.6 × 2.2 mm and vacuum infiltrated twice for 3 min in reaction buffer (50 m*M* N-2-hydroxyethylpiperazine-N′-2-ethanesulfonic acid-KOH, 0.5 m*M* $CaSO_4$, pH 7.2) at 20–22°C. In addition to bypassing stomatal limitations (Steffen et al. 1985), this technique allowed us to eliminate the effects of morphological differences that have been observed between the species (Palta and Li 1979) which could influence gas exchange parameters.

Leaf pieces were then placed in the temperature-controlled reaction chamber of the oxygen monitor containing 2.9 ml of aerated buffer at 20°C. Photosynthetic oxygen evolution was subsequently initiated by supplying light from a 250 W tungsten halogen lamp (Quartzline PAR flood lamp, General Electric Co., Cleveland, OH, USA) with the photon flux density at the surface of the reaction chamber adjusted by using neutral density gradients and by the addition of 0.1 ml of $NaHCO_3$ solution to yield a final concentration of 20 m*M* in the reaction mixture. A 2.5 cm thick water barrier between the light source and the reaction chamber prevented heat build-up. It is important to realize that leaf pieces stirring within the reaction chamber are exposed to light levels as high as that at the surface of the chamber for only a very small percentage of the time. This is due to mutual shading and the random tumbling of pieces which results in less than optimal orientations for interception of

light. Light-limited photosynthetic oxygen evolution was measured at 120 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (400–700 nm) following a 3 min pre-illumination at the same light intensity in the absence of $NaHCO_3$. Light-saturated rates were measured at 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on the same tissue after a 10 min pre-illumination at 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in fresh buffer.

Using this approach, photosynthetic rates were ca 70% of parallel gas exchange determinations at ambient CO_2 and 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ light level (Steffen et al. 1985). These gas exchange rates were nearly identical to published values from potato plants grown under similar conditions and assayed at ambient CO_2 and 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ light level (Ku et al. 1977). The lack of any detectable decline in measured rates of oxygen evolution over the course of the assays demonstrated that any photoinhibition occurring during the assays was not a significant factor in our determinations (Fig. 1). Furthermore the artificially high CO_2/O_2 ratio in the reaction mixture would minimize photorespiration, allowing a good indication of the relative changes in net photosynthetic capacity in response to treatments.

Respiration rates were measured on the same tissue by darkening the reaction chamber and following oxygen uptake. Chlorophyll was extracted from leaf tissue pieces in 96% ethanol and the content was determined according to Wintermans and De Mots (1965). Respiratory oxygen uptake expressed on a chlorophyll basis was added to net photosynthetic oxygen evolution to obtain gross photosynthesis. The basis for this addition is the lack of any evidence that mitochondrial respiration is, in fact, suppressed in the light (Kelly 1983).

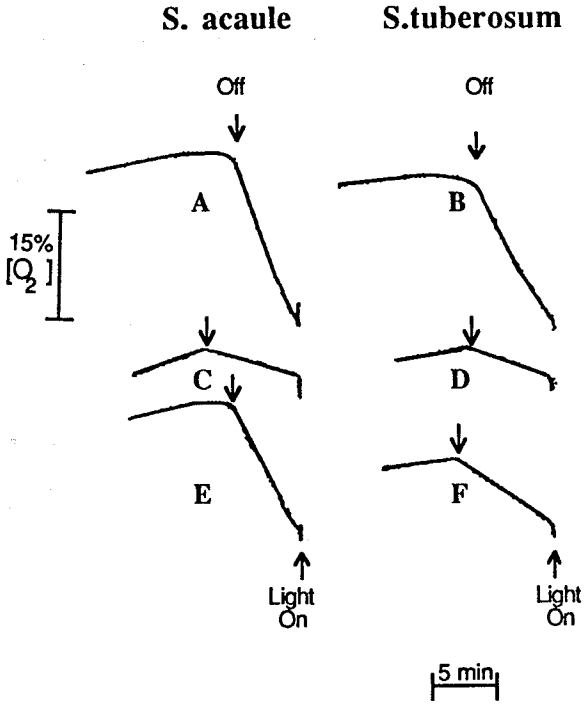

Fig. 1. Typical traces from oxygen electrode in measurements of light- and carbon dioxide-saturated net photosynthetic oxygen evolution (light on) and respiratory oxygen uptake (light off). Chart travel is from left to right. A and B, control plants maintained at 20/15°C; C and D, plants maintained for 24 days under moderate light levels at 5/2°C; E and F, plants maintained for 24 days under low light levels at 5/2°C.

Tab. 1. Comparison of chlorophyll *a/b* ratios of plants maintained at low temperature under different light levels. Sample tissue was from plants grown for 24 days at 5/2°C under either 400 or 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$, moderate and low light, respectively. Initial values represent the means of 12 samples at day zero of treatment. Values at 24 days are the means of 6 replicates ± SE per light treatment.

Species	Initial (day 0)	24 days at 5/2°C	
		Moderate light	Low light
S. tuberosum	4.2±0.10	4.0±0.02	3.9±0.06
S. acaule	3.6±0.06	3.4±0.04	3.4±0.06

The experiment was analysed as a split-split plot design with 3 blocks, 4 light levels, 2 species within light levels and 3 durations. A separate analysis was conducted without the lowest light level, as a qualitatively different response was observed at this light level in *S. tuberosum* (Tab. 2).

Results

A steady loss of total chlorophyll content on a fresh weight or an area basis was observed in all species by light level treatments over time of exposure to low temperature. This loss was substantial after 24 days at the higher light level, resulting in a 49 and 38% reduction, on a fresh weight basis, in *S. tuberosum* and *S. acaule*, respectively. This is more than double the decline observed in both species under low light levels (Fig. 2). No change in chlorophyll *a/b* ratios was seen in either species at either light level (Tab. 1). This is in contrast to the characteristic shade plant response seen in plants at higher temperatures which gave a significant decline in chlorophyll *a/b* ratios at low light levels (data not shown).

Within the two light levels, the incident light at the leaflet varied within the plant canopy. The relationship between incident light level at the leaflet during low temperature treatment and photosynthesis was quite different between *S. acaule* and *S. tuberosum* specifically at light levels below ca 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 3). *S. acaule* showed a linear decline in photosynthetic capacity as incident light levels increased from 5 to 540 $\mu mol \cdot m^{-2} \cdot s^{-1}$. *S. tuberosum*, in contrast, showed a curvilinear response with a light level optimum at ca 50

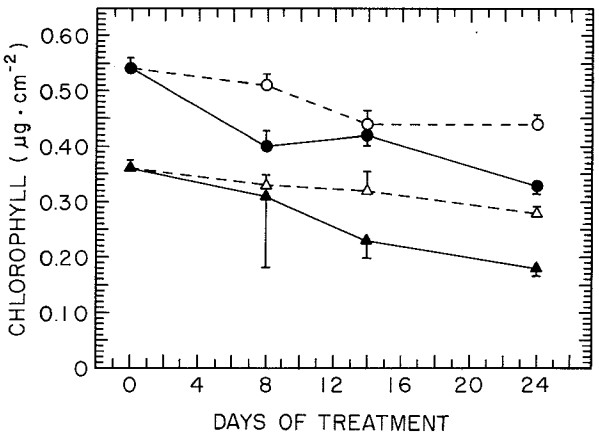

Fig. 2. Changes in chlorophyll content during growth at low temperature and different light levels. Day zero represents the transfer of eight-week-old plants to various treatment conditions. Canopy light levels during growth: Closed symbols, 400 μmol · m^{-2} · s^{-1}; open symbols, 40 μmol · m^{-2} · s^{-1}. Plant material: Triangles, *S. tuberosum*; circles, *S. acaule*. Bars equal SE of 6 replications.

Tab. 2. Analysis of variance on effects of measured incident light level, species and treatment duration on gross light- and carbon dioxide-saturated photosynthetic oxygen evolution. Separate analyses were performed on all 4 light levels and without light level I. df, Degrees of freedom; ns, Not Significant at 5% level; *, significant at 5% level; **, significant at 1% level; ***, significant at 0.1% level.

Source of variation	Light levels I, II, III, IV		Light levels II, III, IV	
	df	Mean square	df	Mean square
Block (B)	2	97^{ns}	2	133^{ns}
Light (L)	3	7088***	2	10606***
Error a (B × L)	6	255^{ns}	4	357^{ns}
Species (S)	1	7546***	1	1812*
L × S	3	1446*	2	34^{ns}
Error b (B × L × S)	8	274^{ns}	6	247^{ns}
Duration (D)	2	2748***	2	2703***
L × D	6	288^{ns}	4	265^{ns}
S × D	2	312^{ns}	2	252^{ns}
L × S × D	6	123^{ns}	4	92^{ns}
Error c (B × L × S × D)	32	329^{ns}	24	268^{ns}

μmol · m^{-2} · s^{-1}. As light levels increased above 50 μmol · m^{-2} · s^{-1}, there was a linear decline in photosynthetic capacity similar to that observed in *S. acaule*. This different behavior of the two species was already apparent at the first sampling date (Fig. 3) and remained consistent throughout the acclimation treatment. In further analysis of light-saturated and light-limited photosynthesis the 400 and 40 μmol · m^{-2} · s^{-1} light treatments were further subdivided to get a total of 4 light regimes based on actual incident light levels at the surface of the sampled leaflet: I, 5–20; II, 21–50; III, 51–200; and IV, 201–450 μmol · m^{-2} · s^{-1}. These groupings allowed 3 observations within each category.

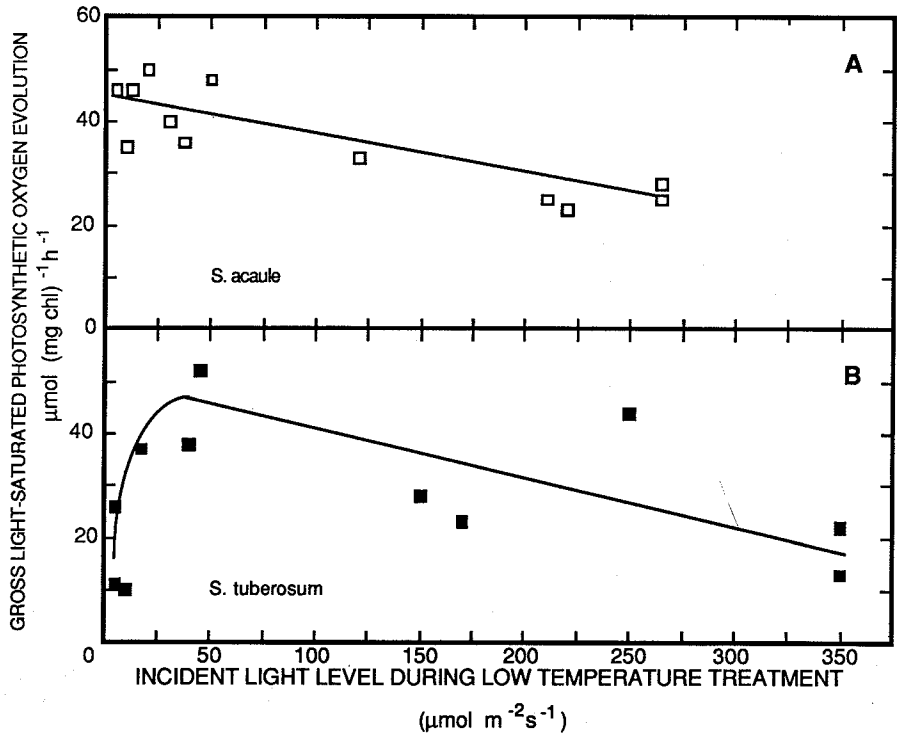

Fig. 3. Correlations on day eight of cold treatment between actual incident light levels at the leaflet surface and light- and carbon dioxide-saturated gross photosynthetic oxygen evolution. The r^2 value equals 0.73 for *S. acaule*.

Tab. 3. Mean separation of treatment effects by Duncan's multiple range test at the 5% level, for photosynthesis expressed as percentages of control. Means within a treatment followed by the same letter are not significantly different at the 5% level.

Treatment	Means
Light level	
II	83[a]
I	59[b]
III	53[b]
IV	36[c]
Species	
S. acaule	68[a]
S. tuberosum	48[b]
Duration, days	
8	65[a]
14	63[a]
24	45[b]

There was a consistent and highly significant effect of increasing light levels and duration of light and temperature treatment on depression of photosynthetic capacity in both species (Fig. 4, Tab. 2). The exception was light level I which showed a greater inhibition than expected (Tab. 3) due to the differential response of *S. tuberosum* to very low light levels (Fig. 4A). Furthermore, when light level I was dropped from the analysis the light × species interaction was eliminated (Tab. 2). At the highest light level, the gross light-saturated photosynthesis showed a sharp decline to 52 and 37% of control by day eight and to 26 and 22% of control by day 24 in *S. acaule* and *S. tuberosum,* respectively (Fig. 4D). After 24 days at light level III (Fig. 4C) photosynthesis had declined to 44 and 31% of control in *S. acaule* and *S. tuberosum,* respectively, while at light level II (Fig. 4B) the decline was only to 76 and 61% of control, respectively. There were only small differences between light levels I and II, in the decline of photosynthesis (68 vs 76% of control) in *S. acaule* (Fig. 4A, B). However, a dramatic difference between these two light levels was observed (35 vs 61% of control) in *S. tuberosum* (Fig. 4A, B).

In general, there was a significantly greater inhibition in *S. tuberosum* than *S. acaule* over all light levels and durations (Fig. 4, Tab. 3). While a part of this difference between the species can be explained by the difference in response to very low light levels (Fig. 4A), dropping light level I from the analysis (Tab. 2) still shows a significant difference between the species ($P = 0.035$). The differences between the species appeared to be a matter of degree with the exception of incident light levels below 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$, where a different type of injury mechanism or threshold effect seemed to be operational (Fig. 3). At this low light level, photosynthesis in *S. tuberosum* dropped to 33% of control at day 8 and then remained at about this level through day 24, while *S. acaule* declined only gradually to 68% of control by day 24 (Fig. 4A).

Considerable variation in determinations of gross light-limited photosynthetic oxygen evolution resulted in no significant treatment effects at the 5% level. There was considerably less inhibition apparent at the end of

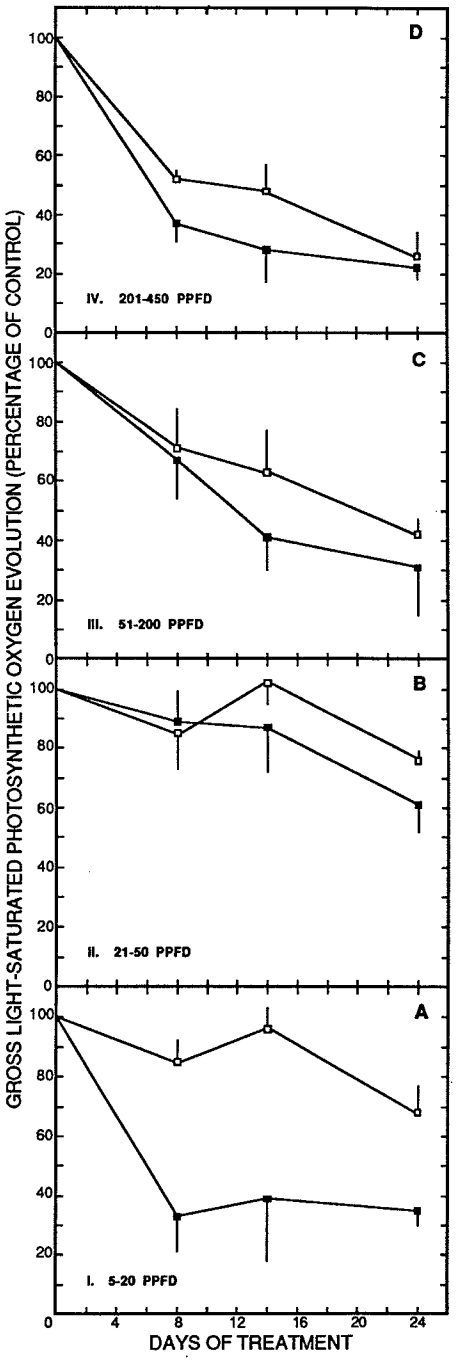

Fig. 4. Effect of light level during maintenance of *S. acaule* (open squares) and *S. tuberosum* (filled squares) at 5/2°C. Bars equal SE of 3 replications. PPFD, photosynthetic photon flux density.

Tab. 4. Effect of 24 day exposure of plants to low temperature and various light levels on gross light-limited and carbon dioxide-saturated photosynthetic oxygen evolution. Measured incident light levels are: I, 5–20; II, 21–50; III, 51–200; and IV, 201–450 μmol · m^{-2} · s^{-1}. Values are expressed as percentage of control: *S. acaule* 13.1 ± 2.46 μmol · (mg chl)$^{-1}$ · h^{-1}; *S. tuberosum* 11.0 ± 1.62 μmol · (mg chl)$^{-1}$ · h^{-1}. Data are means ± SE of 3 observations.

Species	Light levels I	II	III	IV
S. acaule	106±9	106±5	99±11	74±27
S. tuberosum	71±19	89±26	65±4	54±10

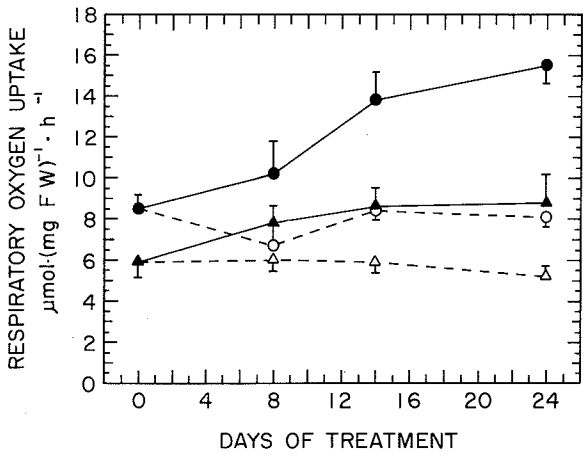

Fig. 5. Effect of growth at low temperature (5/2°C) and two light levels on rates of dark respiration. The meaning of symbols and error bars is the same as in Fig. 2.

the 24 day treatment, however, than was seen in light-saturated assays (compare data in Fig. 4 with Tab. 4). Again a much smaller decline was seen in *S. acaule* than in *S. tuberosum* over all light levels and the difference between the two species was significant at the 10% level. Similar differences were observed at the other durations.

An increase in respiration rates in both species at the higher light levels was found (Fig. 5). This increase was greater in *S. acaule* (ca 80% over control) than in *S. tuberosum* (ca 50% over control). However, no increase was found at the low light levels in either species (Fig. 5).

Discussion

The results of the present study show that the photosynthetic apparatus of *Solanum* species, a plant material considered to be chilling-insensitive, suffers a significant amount of injury during exposure to a low temperature (chilling), acclimation environment. This injury was found to be light-dependent (Fig. 4, Tab. 3). Our results show that at the moderate light levels and temperatures commonly used for experimental cold acclimation, there is a marked inhibition of photosynthetic capacity in both species. Furthermore the inhibition, within limits, could be reduced by lowering the incident light levels. This inhibition of photosynthesis was independent of chlorophyll loss and stomatal restrictions since rates were calculated on a chlorophyll basis and the stomatal effects were eliminated by the technique used. Several previous studies have documented the light-dependent photoinhibition at low temperatures in chilling-sensitive species or cold hardy tree species (for reviews see Öquist 1983 and Powles 1984). The present study extends these observations to a chilling-insensitive herbaceous species.

The mechanism(s) of photoinhibition and strategies for its prevention in potato species is/are as yet undocumented. In numerous other plant materials, considerable evidence is accumulating which supports Osmond's proposal that whenever the rate of excitation trapping at the photochemical reaction centers exceeds the rate of transfer through the electron transport system, damage to the photosynthetic apparatus occurs (Osmond 1981). Powles (1984) has classified mechanisms for avoidance or tolerance of photoinhibition into 3 broad classes: biophysical dissipation of excess energy, metabolism of reactive oxygen species, and morphological adaptations to reduce light-trapping under stress conditions. It is likely that many plants utilize a combination of different types of protection. Comparative studies of closely-related species which differ in their level of stress tolerance could provide some clues as to the relative importance of these mechanisms. This information could be useful in the improvement of crop plants.

The two species used in the present study showed a marked differential response. The inhibition in nearly all measured parameters of photosynthetic capacity was greater in the cold-sensitive *S. tuberosum* than in the cold-tolerant *S. acaule* (Figs 2 and 4, Tab. 4). This lends support to our working hypothesis that an important component of the ability to frost acclimate is the ability to prevent light-dependent disruption of photosynthetic metabolism at low, non-freezing temperatures. The reason for the differential response of the two species may be due, in part, to the fact that cold-tolerant species such as *S. acaule* have multiple palisade layers in contrast to a single palisade layer in the leaves of *S. tuberosum* (Palta and Li 1979). The thicker palisade layer in *S. acaule* could, by internal shading, reduce light-dependent photoinhibition in the lower palisade and spongy parenchyma cells.

The overall greater decline in light-saturated vs light-limited rates suggests that a substantial amount of the photoinhibition observed here may not be a result of impaired light-trapping capacity. It is interesting that these results are parallel to those of Martin and Ort (1982) who concluded that in dark chilling of tomato, there is little reduction in water oxidation at photosys-

tem II. The much more dramatic increase in respiration rates in *S. acaule* at high light levels (Fig. 5) could be related to the relative ability of the species to accumulate respiratory intermediates from photosynthesis, which are then rapidly metabolized when the tissue is equilibrated to the higher assay temperature (Maciejewska et al. 1984). A lack of inhibition of respiratory metabolism at low temperature by other than effects on enzyme reaction rates is also suggested by these results.

To our knowledge, this is the first comparative study using genetically-related, cold-tolerant herbaceous species, to examine the effects of light and low, non-freezing temperatures on impairment of photosynthetic capacity. Since this chilling treatment leads to cold acclimation in *S. acaule* and not in *S. tuberosum,* the results suggest that the maintenance of photosynthetic capacity may be a factor in the ability to acclimate. Further investigation into the stability of the photosynthetic apparatus from cold-tolerant species which can acclimate and cold-sensitive species which cannot, could provide important insights into the adaptive mechanisms which protect certain potato species in extreme environments.

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