PHYSIOLOGIA PLANTARUM 94: 51–56. 1995

Balancing photosynthetic light-harvesting and light-u capacities in potato leaf tissue during acclimation to growth temperatures

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Steffen, K. L., Wheeler, R. M., Arora, R., Palta, J. P. Balancing photosynthetic light-harvesting and light-utiliza tissue during acclimation to different growth temperatures.

We investigated the effect of temperature during growt relationship between light-harvesting capacity, indicated b and light-utilization potential, indicated by light- and bica thetic oxygen evolution, in *Solanum tuberosum* L. cv. No transplanted and grown at 20°C for 2 weeks before transfe for 6 weeks. After 4 weeks of the temperature treatments, area were one-third higher in plants grown at 12°C vs versely, chlorophyll content per area in tissue grown at 12 that of tissue grown at 28°C at 4 weeks. Photosynthe common temperature of 20°C and expressed on a chlo proportional to growth temperature. Leaf tissue from plant had photosynthetic rates that were 3-fold higher on a chlo ble tissue from plants grown at 28°C. These results su between light-harvesting capacity and light-utilization po sponse to the growth temperatures examined. The role of t photoinhibition is discussed.

Key words – Acclimation, chlorophyll, light, photoinhibit respiration, *Solanum tuberosum,* temperature.

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Introduction

Plants can adapt photosynthetic function to a wide range of prevailing environmental conditions. It is well known that plants acclimated to different growth temperatures shift the temperature optima of photosynthesis to more

energy, while in a sun environm light energy is reduced.

Osmond (1981) proposed th versible, light-dependent inhib would occur under environmer amount of light energy harveste

ses (Bolhar-Nordenkampf et al.
qvist 1992). Willow leaves in a
ce a midday inhibition of variable
nce (F_v/F_m) of 15% at 23°C and
Sjöström 1990). Photoinhibitory
o reduce the efficiency of photo-
sion to dry matter in overwinter-
to 66% (Farage and Long 1991).
t studies have demonstrated a
een light level and temperature
light and/or decreased ambient
n an increased susceptibility to
et al. 1984, Steffen and Palta
1991).

ronment, temperature generally
viding a period of acclimating,
that precede stress conditions,
c adjustment. Numerous studies
cclimated to low, nonstress tem-
tolerance to chilling (Somersalo
, Nie et al. 1992) and high light
ta 1989, Falk et al. 1990). Many
used on the repair mechanisms or
ystems in cold-acclimated chlo-
response to changing light and
would be adjustments within the
s, which would balance the light-
pacity with the light-utilization

designed to examine changes in
s involved in light energy har-
y utilization in clonal *Solanum*
o different growth temperatures.
nds the initial investigations by
nich reported the effect of growth
period on various indicators of
otal dry matter accumulation and

s

intained as described previously
. In brief, *Solanum tuberosum* L.
e propagated as clonal lines on
ussey and Stacey 1981) and then
ontaining 1:1 (v/v) peat-vermic-
shed at 20°C in a 12-h photope-
amps (Sylvania/GTE, Danvers,

complete nutrient solution (Hammer et al. 1978). Following transfer to temperature treatments, leaf tissue was harvested at 2-week intervals for determinations of fresh weight, chlorophyll content, net photosynthetic oxygen evolution and respiratory oxygen uptake. For use in assays two leaf disks (16 mm in diameter) were excised from a single terminal leaflet at the top of the plant canopy, which was ca 80–90% in area of the most fully expanded leaflet on that plant. Each of the above determinations was replicated six times. Total soluble protein levels were determined at 6 weeks on a combined crude leaf extract from each of the growth temperature treatments, with the exception of the 24°C treatment which was accidentally discarded and lost.

Assays

Assays of photosynthetic oxygen evolution and respiratory oxygen uptake were conducted using a YSI oxygen electrode (Yellow Springs, OH, USA) at weeks 2 and 4 of growth temperature treatments and the methods were essentially as described previously (Steffen and Palta 1986). Leaf tissue was placed into 3.0 ml of assay buffer in a water-jacketed electrode chamber maintained at the growth temperature of the tissue to be assayed. First, respiration was measured for 8 min at the temperature under which the plants were grown. Photosynthesis was then measured for 12 min at saturating light levels of 1 750 μmol m^{-2} s^{-1} PPFD from a 250-W tungsten halogen lamp (General Electric, Cleveland, OH, USA). Following these assays the electrode chamber was equilibrated to a common temperature of 20°C and light-saturated photosynthesis was again measured for 12 min on the same tissue. Reversing the order of the assays had no effect (data not shown). Chlorophyll was extracted from the leaf tissue following assays and quantitated spectrophotometrically in 96% ethanol according to Wintermans and Demots (1965). Soluble protein levels from crude extracts were determined according to Bradford (1976). All chemicals were purchased from Sigma.

Results

As previously noted (Wheeler et al. 1986) the degree of leaf expansion was the most obvious morphological difference across growth temperature treatments. Leaf size was inversely related to temperature with cooler temperatures resulting in larger individual leaflets. There was also an inverse relationship between growth temperature and leaflet fresh weight per area with leaflets grown at

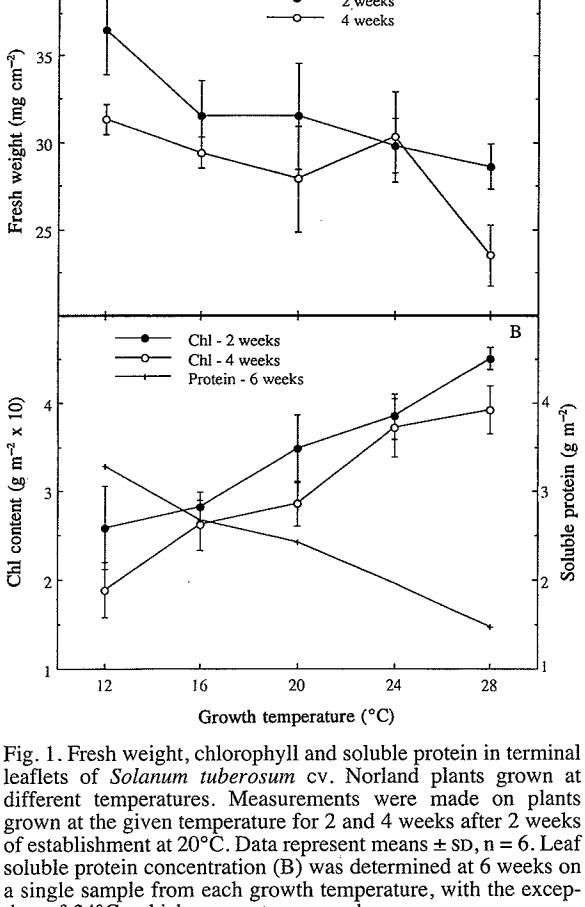


Fig. 1. Fresh weight, chlorophyll and soluble protein in terminal leaflets of *Solanum tuberosum* cv. Norland plants grown at different temperatures. Measurements were made on plants grown at the given temperature for 2 and 4 weeks after 2 weeks of establishment at 20°C. Data represent means ± SD, n = 6. Leaf soluble protein concentration (B) was determined at 6 weeks on a single sample from each growth temperature, with the exception of 24°C, which was not measured.

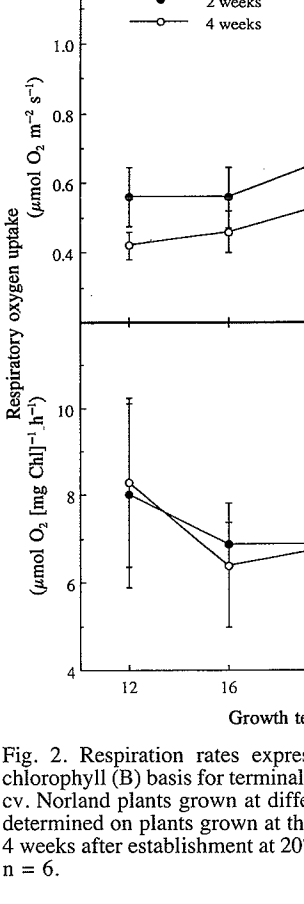


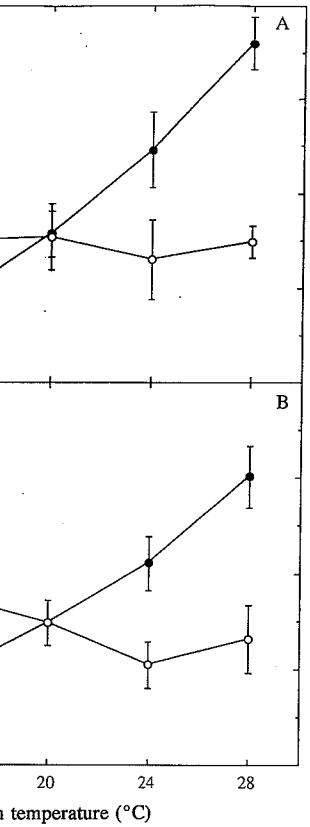
Fig. 2. Respiration rates expres
chlorophyll (B) basis for terminal
cv. Norland plants grown at diffe
determined on plants grown at th
4 weeks after establishment at 20
n = 6.

per unit area compared to tissue from the 28°C growth temperatures after 2 and 4 weeks of growth, respectively (Fig. 1B).

Respiration rates on a leaflet area basis and measured at the tissue growth temperature, decreased 56 and 46% at 2 and 4 weeks, respectively, as growth temperatures decreased from 28 to 12°C (Fig. 2A). On a chlorophyll basis, however, respiration from tissue grown at all temperatures was similar at both 2 and 4 weeks (Fig. 2B).

Rates of light- and bicarbonate-saturated net photosynthetic oxygen evolution on an area basis and measured at the growth temperature, declined 38 and 37% at 2 and 4 weeks, respectively, as the growth temperature of the tissue decreased from 28 to 12°C (Fig. 3). However, when the same tissue was assayed at a standard temper-

synthetic rates were determine
of 20°C and expressed on a
inverse relationship betwee
photosynthetic capacity was
sampling date, tissue grown a
tosynthetic capacity per chl
greater than that grown at 28°
increased to 3-fold in tissue
the extremes of growth temp
(Fig. 4B). In order to give a re
growth temperatures, plant ti
20°C was first assayed at its
and then at 28°C (Tab. 1). Pla
at 20 or 28°C demonstrate
photosynthesis when assayed
When plants grown at 20°C
temperature (28°C) there wa



n temperature (°C)

xygen evolution expressed on an
flets of *Solanum tuberosum* cv.
ent growth temperatures. Oxygen
plants grown at the given temper-
ks after establishment at 20°C and
f growth (GT) and at 20°C. Data

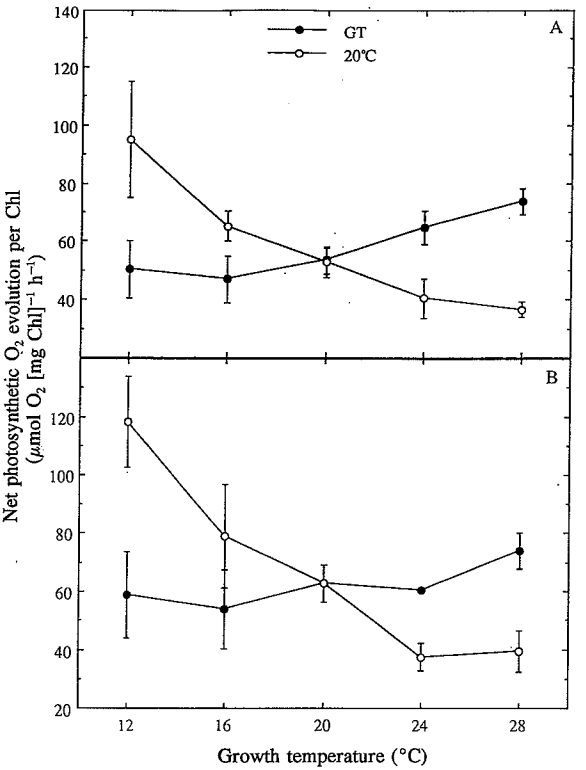


Fig. 4. Net photosynthetic oxygen evolution expressed on a chlorophyll basis from nearly fully expanded leaf tissue of *Solanum tuberosum* cv. Norland plants grown at different temperatures. Oxygen evolution was determined on plants grown at the given temperatures for 2 (A) and 4 (B) weeks after establishment at 20°C and measured at the temperature of growth (GT) and at 20°C. Data represent means ± SD, n = 6.

capacity per chlorophyll as
emperature is decreased from
relationship between temper-
apacity became apparent when
n of the five growth treatment
8°C, was assayed at a common
4, Tab. 1). Respiration rates
basis and measured at tissue
he same in tissue grown at 12
e growth temperatures result-
s (Fig. 2). While it was not
gen uptake at a common tem-
nave undoubtedly shown in-

explained by a 2-fold decrease in chlorophyll content and a nearly 2-fold increase in soluble protein content. For example, at 4 weeks, as growth temperature decreased from 28 to 12°C, chlorophyll content per area decreased 2.1-fold, representing a probable decrease in light-harvesting capacity (Fig 1B). Conversely, as growth temperature decreased, soluble protein content per area increased 2.2-fold at 6 weeks (Fig. 1B), indicating an increase in enzymatic capacity to utilize and thus dissipate photochemical energy.

These results are consistent with the findings of Öquist

Tab. 1. Comparison of net photosynthetic capacity following 4 weeks of growth at 20 or 28°C using reciprocal assay temperatures on the same leaflet tissue. Data represent means ± SD, n=6.

and Huner (1993) who demonstrated that a critical determinant in plant avoidance of photoinhibitory stress at low temperatures is the ability to increase light- and carbon-dioxide-saturated photosynthetic capacity. The changes we observed in photosynthetic capacity per chlorophyll are similar to those documented by Öquist and Huner in a comparison of nonacclimated (20/15°C) vs cold-acclimated (5/5°C) rye. If their photosynthetic rates per unit area are converted to a chlorophyll basis, approximately a 2-fold increase in photosynthetic capacity can be calculated for cold-acclimated vs nonacclimated plants. On an area basis, however, this difference increased to 5.6-fold which was in contrast to our results, showing no difference in photosynthetic capacity per area between potato leaf tissue grown at 12 and 28°C (Fig. 3).

Much of this discrepancy in photosynthetic capacity per unit of chlorophyll could be explained by the differential effect of the low temperature acclimation on chlorophyll content per area between rye and potato plants. We observed a 2-fold decrease in chlorophyll concentration (Fig. 1B) in potato during low temperature treatment (12 vs 28°C) while rye plants demonstrated a 38% increase with decreased growth temperature (5 vs 20°C). Low growth temperatures are known to result in a decrease in chlorophyll accumulation with marked species differences existing for the temperature threshold of this inhibition (Hodgins and Öquist 1989). It is also possible that significant species differences exist between grasses and broadleafs in their potential for leaf cell expansion at low temperature which would alter chlorophyll concentration per area due to expansion growth and dilution of cell contents. The reduction of chlorophyll content per area represents a potential loss of light harvesting capacity at the lower temperatures. This reduction could act to balance photosynthetic photon flux through the chloroplast during acclimation to decreased growth temperature. We have previously shown a large decrease in the amount of total chlorophyll relative to levels of the light-harvesting chlorophyll binding complex of photosystem II in photosynthetic tissue grown at 12°C vs that grown at 24°C (Steffen and Palta 1987). By contrast, rye plants exposed to cold-hardening temperatures demonstrate an increase in chlorophyll per plastid and no change in thylakoid membrane composition with the exception of a shift from oligomeric to monomeric forms of the light harvesting chlorophyll binding complex (Huner et al. 1987, Krupa et al. 1987). However, both of these responses could conceivably result in a decrease in chlorophyll antennae size and thus a decrease in light-harvesting efficiency.

synthetic apparatus and maintain
tivity during low temperature ac
Palta 1986). However, in contras
here, when potato plants are expo
changes of temperatures, there is
decrease in photosynthetic capaci
frame of 2 to 3 weeks (Steffen an
studies have investigated the effe
in the thermal growth environm
between light energy trapping an
ies of low temperature acclimatio
parisons of plants developed unde
cold acclimating temperatures (2
sented here suggest an important
balance energy flux through the c
gradual changes in growth temp

Acknowledgments – We would like
ance of A.Y. Abdallah on this project
by the College of Agricultural and
Wisconsin, Madison, WI 53706, US
Agreements NCC 2-136 and NCC 2

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