

Photosynthetic Adaptation to Temperature

I. General features of photosynthetic carbon assimilation versus temperature

A. Plants can photosynthesize across a broad range (0 to $\sim 50^{\circ}\text{C}$) but are limited across this range by different things (see lecture on overview of photosynthesis):

1. at low temperatures ($0\text{--}10^{\circ}\text{C}$), - enzyme limited, phosphate limited at the chloroplasts
2. between $10\text{--}35^{\circ}\text{C}$, - mostly CO_2 diffusion limited (e.g. RuBisco is not saturated), RuBP regeneration limited (e.g. energy from electron transport cannot regenerate RuBP fast enough), or starch/sucrose utilization limited (e.g. build-up causes photosynthesis to decline)
3. above $35\text{--}40^{\circ}\text{C}$, - proteins can denature, membranes can become deformed (deleterious effects)

B. Optimal temperatures for GROSS photosynthesis in plants are $15\text{--}40^{\circ}\text{C}$, but above $\sim 10^{\circ}\text{C}$, dark respiration goes up and NET photosynthesis goes down (Fig.).

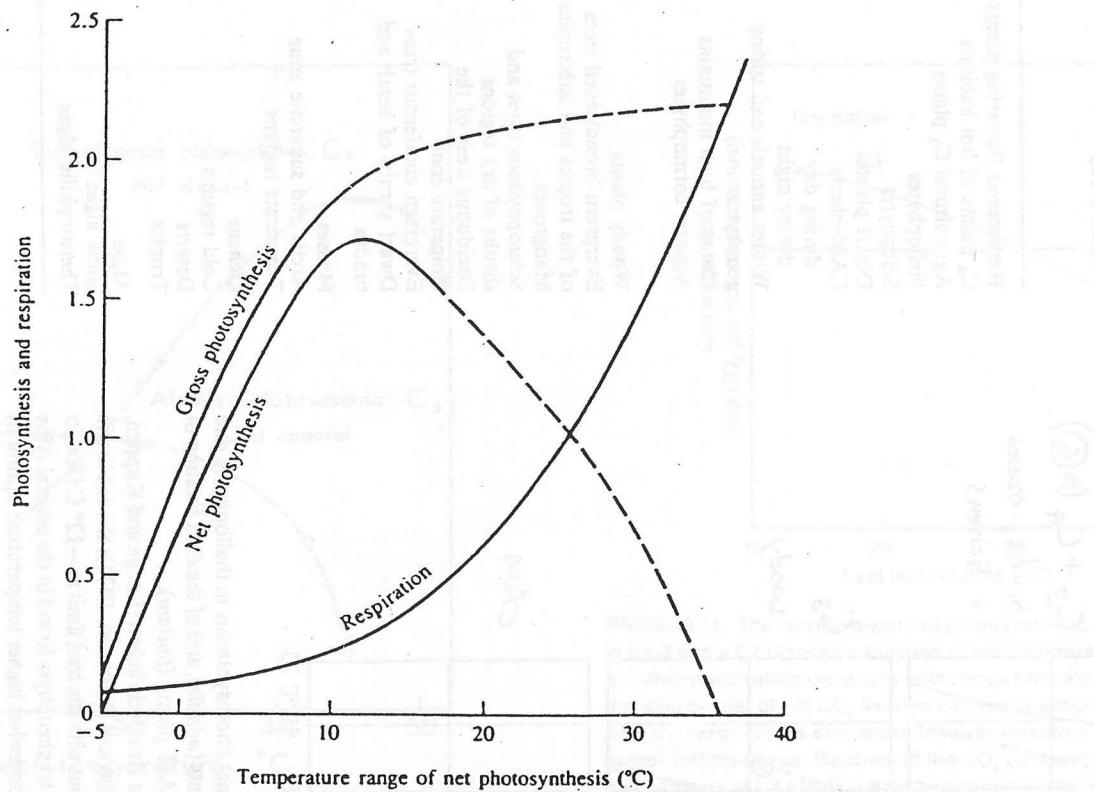


Figure 5.12 Effects of temperature on photosynthesis, respiration, and net or apparent photosynthesis of Swiss stone pine seedlings. Solid lines are from actual measurements; broken lines are estimated. (After Tranquillini, 1955; from Kramer and Kozlowski, 1979, by permission of Academic Press.)

C. Photosynthesis vs. temperature curves are generally bell shaped (Figs.)

1. plants with different photosynthetic pathways (C_3 , C_4 , and CAM) differ in their responses (Fig.)

D. As far as photosynthesis is concerned, it is generally thought that:

1. LOW temperature (non-freezing) responses are mediated by changes in root membrane characteristics which in turn influence water and nutrient transport that will effect photosynthesis - INDIRECT EFFECTS

Table 2.11. Temperature response of net photosynthesis under conditions of ambient CO₂ and light saturation. Compiled from data of numerous authors

Plant group	Low-temperature limit for CO ₂ uptake (°C)	Temperature optimum of Ph _n (°C)	High-temperature limit for CO ₂ uptake (°C)
Herbaceous flowering plants			
C ₄ plants of hot habitats	+ 5 to 10	30–40 (50)	50–60
Agricultural C ₃ plants	- 2 to 0	20–30 (40)	40–50
Heliophytes	- 2 to 0	20–30	40–50
Sciophytes	- 2 to 0	10–20	ca. 40
Desert plants	- 5 to 5	20–35 (45)	45–50 (60)
CAM plants during day	- 2 to 0	(20) 30–40	45–50
during night	- 2 to 0	10–15 (23)	25–30
Winter annuals and spring geophytes	- 5 to - 2	10–20	30–40
Plants of high mountains	- 6 to - 2	15–25	38–42
Aquatic cormophytes	ca. 0	(15)	20–30 (35)
Woody plants			
Evergreen broadleaved trees of the tropics and subtropics	0 to 5	25–30	45–50
Mangroves	0 to 5	25–30	ca. 40
Sclerophyllous trees and shrubs of dry regions	- 5 to - 1	20–35	42–45
Deciduous trees of the temperate zone	- 3 to - 1	20–25	40–45
Evergreen coniferous trees	- 5 to - 3	10–25	35–42
Dwarf shrubs of heath and tundra	ca. - 3	15–25	40–45
Mosses	Arctic and subarctic zone	ca. - 8	5–12
	Temperate regions	ca. - 5	10–20
Lichens		ca. 30	30–40
Cold regions	- 10 to - 15	8–15 (20)	25–30
Deserts	ca. - 10	18–20	38–45
Tropics	- 2 to 0	ca. 20	25–35
Algae			
Snow algae	ca. - 5	0–10	30
Thermophilic algae	20 to 30	45–55	65

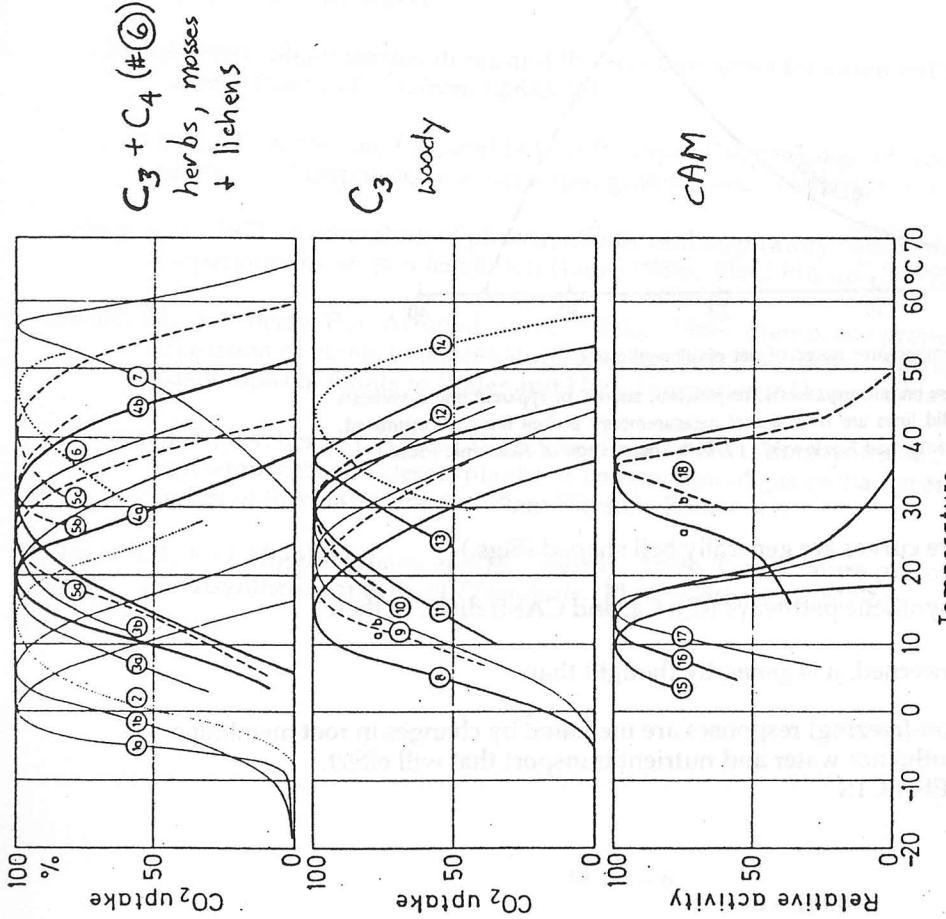


Fig. 3.35. Examples of the temperature-dependence of net photosynthesis in thallophytes and herbaceous tracheophytes (*top graph*) and in woody plants (*middle*), and of the dark fixation of CO₂, and the photosynthetic primary processes in CAM plants (*bottom*).
 1, Lichens and mosses; a, *Lecanora melanophthalma*, an Antarctic lichen (Lejege and Kappel, 1972); b, *Cetraria nivalis*, a subarctic-alpine lichen (Kallio and Heinonen, 1971); the subarctic tundra moss *Rhacomitrium lanuginosum* is similar to b but with the cold limit at -12°C (Kallio and Heinonen, 1973). 2, *Oxyria digyna*, an arctic-alpine tracheophyte found in the central Alps at 2500 m (Pisek et al., 1969); arctic ecotypes have a somewhat higher temperature optimum (Billings et al., 1971). 3, C₃ grain crops: a, wheat (Sawada and Miyachi, 1974; Vong and Murata, 1977); b, rice (Vong and Murata, 1977). 4, dicotyledonous crops: a, potato (Lundegårdh, 1927; Winkler, 1961); b, soybean (Ludlow and Wilson, 1971a, b). 5, C₄ grain crops: a maize varieties for cool climates (Winkler et al., 1975); b, maize varieties for warmer regions (Moss, 1963); c, *Sorghum vulgare*, Arizona (El-Sharkawy and Hesketh, 1964). 6, *Tidesstroma oblongifolia*, a summer-annual C₄ desert plant, Death Valley (Pearcy et al., 1971). 7, *Synechococcus lividus*, a thermophilic blue-green alga, high-temperature clone (Sheridan and Ulik, 1976).

2. HIGH temperature responses are mediated by changes in leaf-level characteristics (e.g. leaf water deficits that influence stomatal closure, changes in photosystem integrity) which in turn influence photosynthesis - DIRECT EFFECTS

II. Photosynthetic temperature response in plants from contrasting thermal habitats

A. Comparison of *Atriplex sabulosa* (C₄), *A. glabriuscula* (C₃) and *Tidestromia oblongifolia* (C₄) over very warm to hot temperatures

1. *A. sabulosa* native of Scandinavian maritime habitats (20°C day time max)
2. *T. oblongifolia* native of Death Valley floor (45°C day time max)

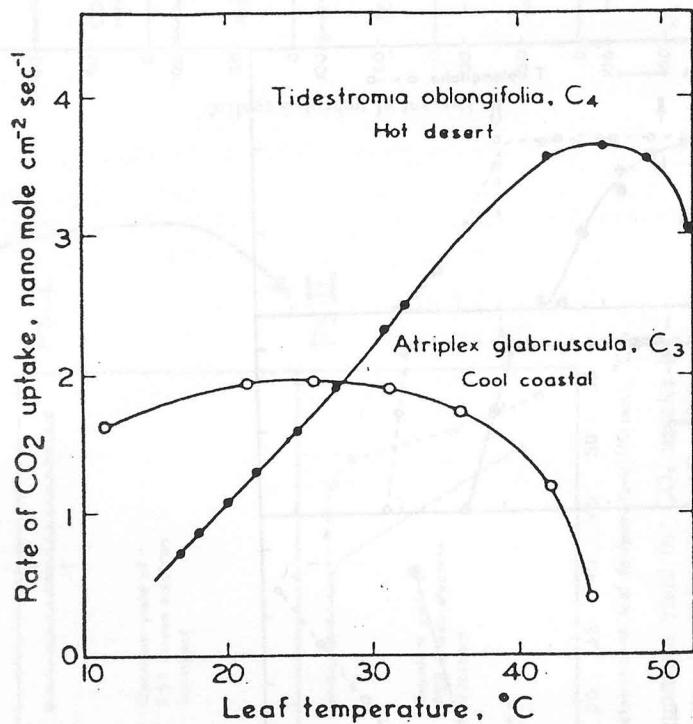


Figure 1 Comparison of the temperature dependences of photosynthesis by whole plants of *Tidestromia oblongifolia* during the summer in Death Valley, California, and *Atriplex glabriuscula*, grown under a temperature regime simulating that of its native coastal habitat. From (38).

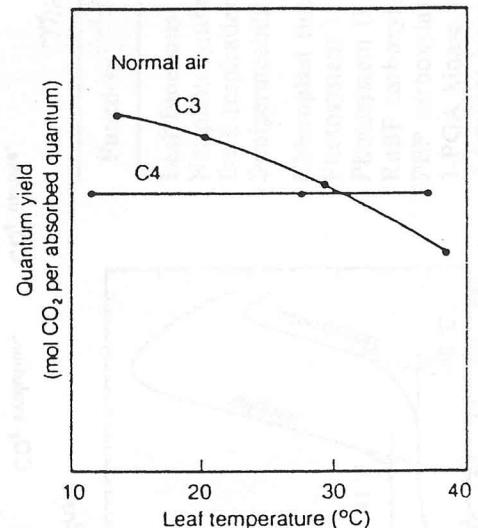
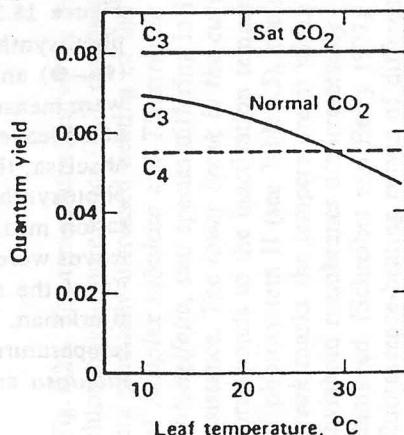


FIGURE 10.14. The quantum yield of photosynthetic carbon fixation in a C₃ and a C₄ plant as a function of leaf temperature. In normal air, photorespiration increases with temperature in C₃ plants and the energy cost of net CO₂ fixation increases accordingly. This higher energy cost is expressed in lower quantum yields at higher temperatures. Because of the CO₂ concentrating mechanisms of C₄ plants, photorespiration is low in these plants, and the quantum yield does not show a temperature dependence. Note, however, that at lower temperatures the quantum yield of C₃ plants is higher than that of C₄ plants. (From Berry and Downton, 1982.)



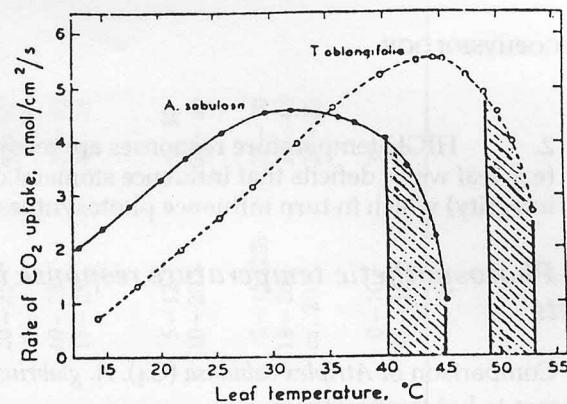
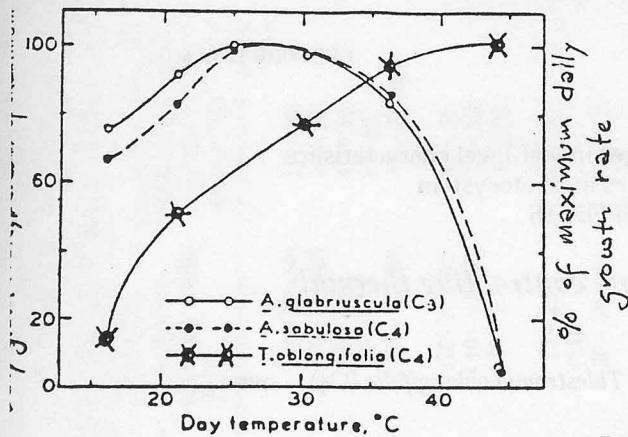


Figure 15.2. Temperature dependence of light-saturated net CO_2 uptake in *Atriplex sabulosa* (grown at 20°C day/15°C night, ●—●) and *Tidestromia oblongifolia* (grown at 45°C day/32°C night, ○—○). Measured quantum flux density was 2000 $\mu\text{E}/\text{m}^2/\text{s}$, CO_2 concentration was 330 $\mu\text{l/l}$, and oxygen concentration was 21% v/v. The shaded areas represent the temperature region in which photosynthesis is unstable, showing a time-dependent decline. Unpublished data of O. Björkman.

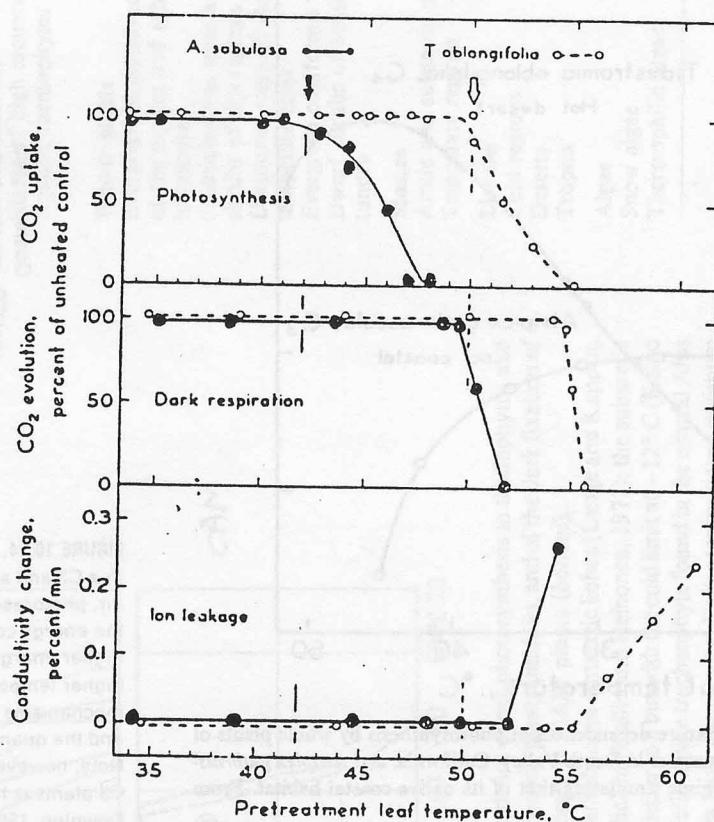


Figure 15.3. Comparison of the heat sensitivity *in vivo* of light- and CO_2 -saturated photosynthetic rate, dark respiration, and ion leakage in leaves of *Atriplex sabulosa* (●—●) and *Tidestromia oblongifolia* (○—○). "Control rates" of photosynthesis were measured at a standard noninhibitory temperature (30°C); the attached, illuminated leaves were subsequently treated for 15 min at the temperature indicated on the abscissa, then quickly returned to the standard noninhibitory temperature, and the photosynthetic rate measured again. Data from Ref. 2. The procedure for the respiration measurements was similar to that used for photosynthesis, except that the leaves were kept in the dark. Ion leakage was measured by the increase in conductivity of the medium in which leaf slices were submerged. Unpublished data of O. Björkman. The solid and open arrows and solid and dashed vertical lines denote the temperatures at which time-dependent inactivation of photosynthesis sets in in *A. sabulosa* and *T. oblongifolia*, respectively.

Photosynthesis declines because of PSII damage

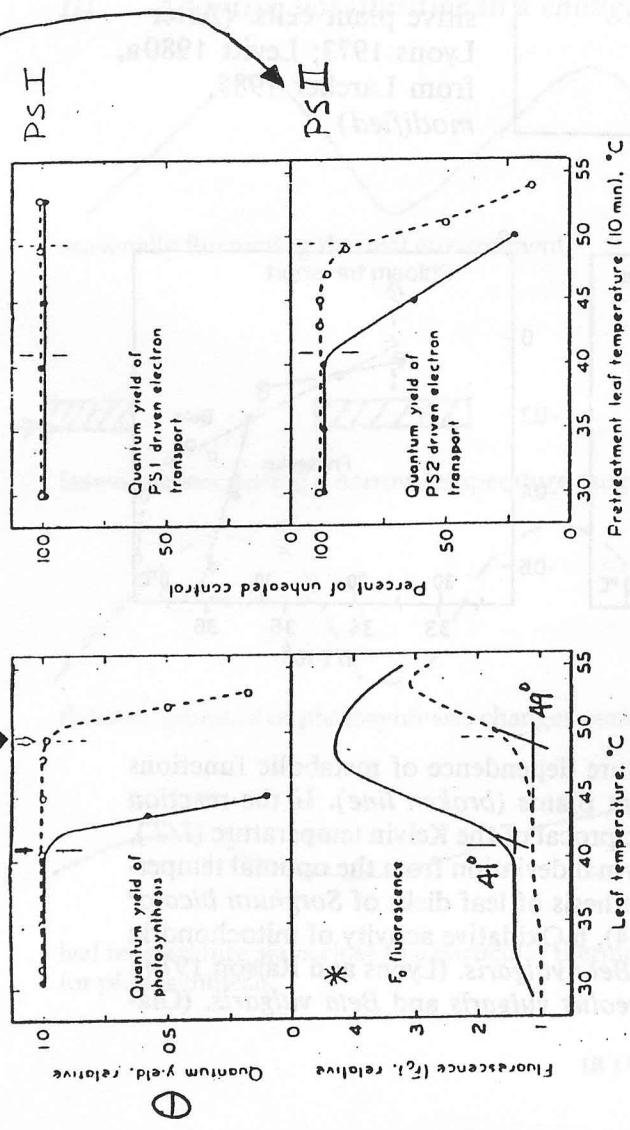


Figure 15.4. Effect of leaf temperature on the quantum yield for CO_2 uptake by intact leaves of *Atriplex sabulosa* (●—●) and *Tidestromia oblongifolia* (○—○) (top left), and of pretreating illuminated detached leaves for 10 min at different temperatures on the quantum yields for photosystem I (PSI)- and photosystem 2 (PSII)-driven electron transport by chloroplasts isolated from these leaves (top and bottom right, respectively). Redrawn from Ref. 7. Also shown is the effect of leaf temperature on the fluorescence yield of detached leaves (bottom left). Redrawn from Ref. 10. Solid and open arrows and solid and dashed vertical lines denote the temperatures at which time-dependent inactivation of photosynthesis sets in in *A. sabulosa* and *T. oblongifolia*, respectively.

* same figure

Thresholds (°C) for 10% inhibition after 10 min heat

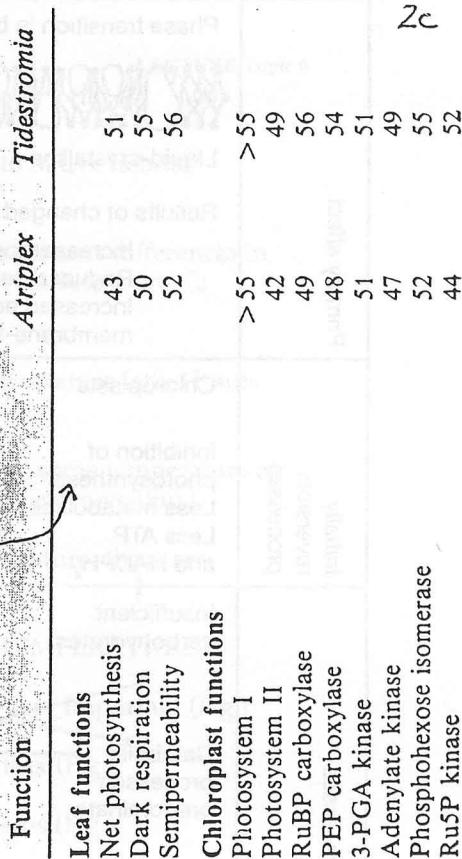


Figure 15.5. Responses of light-saturated photosynthesis, extractable protein, and indicated enzyme activities to pretreatment of illuminated *Atriplex sabulosa* (●—●) and *Tidestromia oblongifolia* (○—○) leaves to different temperatures. From Ref. 9. Solid and open arrows and solid and dashed vertical lines denote the temperature's

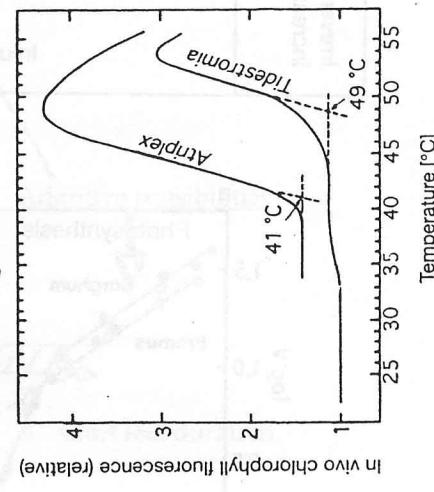


Fig. 6.23. The temperature curve for basic chlorophyll fluorescence (F₀-T diagram) during gradually increased heating of the leaves of *Atriplex sabulosa* and *Tidestromia oblongifolia*, two species differing in heat resistance. The lower break in the curve corresponds to the inactivation temperature of photosystem II (see Table 6.5), the upper break marks the temperature at which the thylakoid membranes are irreversibly damaged. (Schreiber and Berry 1977). For fluorescence-heating curves of different crop plants from tropical and temperate zones, see Smillie and Nott (1979)

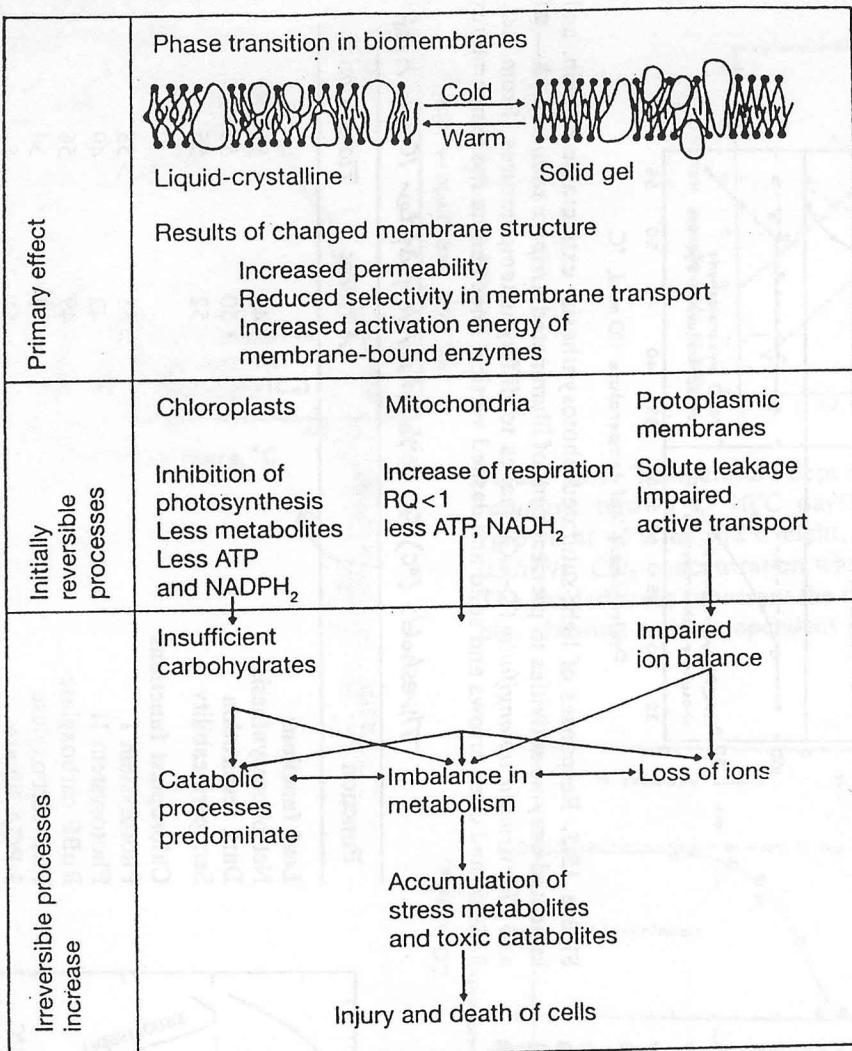


Fig. 6.31. Events and pathways of events leading to damage in chilling-sensitive plant cells. (After Lyons 1973; Levitt 1980a, from Larcher 1985, modified)

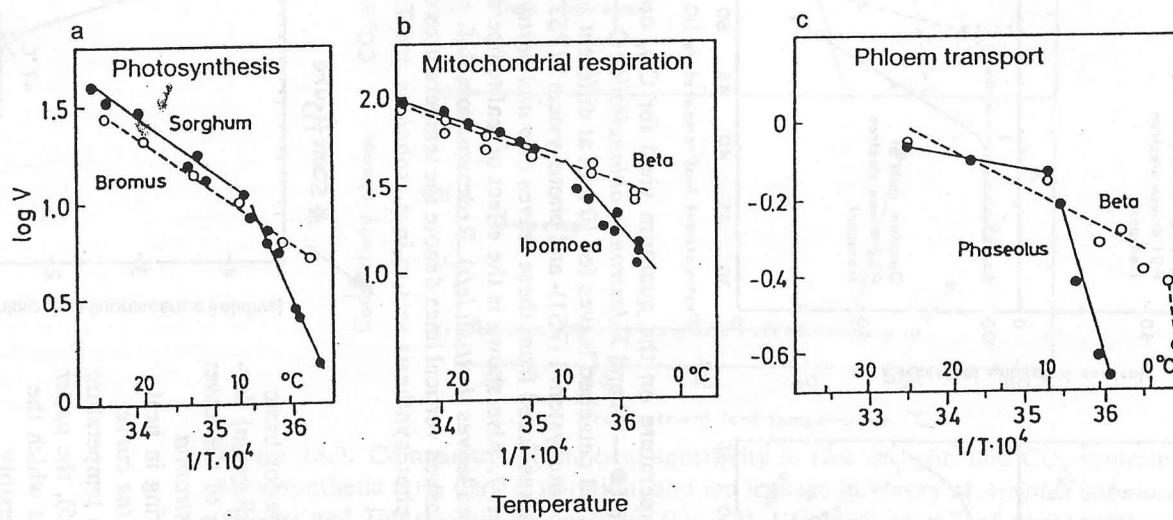


Fig. 6.29a–c. Arrhenius diagrams for the temperature dependence of metabolic functions of chilling-sensitive (*solid line*) and chilling-tolerant plants (*broken line*). If the reaction velocity (V) is plotted logarithmically against the reciprocal of the Kelvin temperature ($1/T$), an inflection in the regression line indicates an abnormal deviation from the optimal temperature coefficient [see formula (2.7)]. **a** Net photosynthesis of leaf disks of *Sorghum bicolor* and *Bromus unioloides*. (McWilliam and Ferrar 1974). **b** Oxidative activity of mitochondria from tubers of *Ipomoea batatas* and from roots of *Beta vulgaris*. (Lyons and Raison 1970). **c** Velocity of phloem transport in petioles of *Phaseolus vulgaris* and *Beta vulgaris*. (Giaquinta and Geiger 1973)

3. growth response is maximized at daytime temperatures similar to native habitat (Fig.)

4. temperature dependence of light saturated photosynthesis shows distinct differences in optimum temperature and upper temperature lethal limits (Fig.); *Tidestromia* and *A. sabulosa* are C₄ plants, thus photosynthesis is not CO₂ limited very (if ever) often

5. dark respiration and/or ion leakage do not account for upper temperature lethal limits (Fig.)

6. quantum yield, fluorescence, and PSII systems decline in activity at same temperature as light saturated photosynthesis; PSI activity does not decline until much higher temperatures (Fig.)

7. some photosynthetic enzymes drop off at upper limit lethal temperature; these are usually light activated enzymes (Fig.)

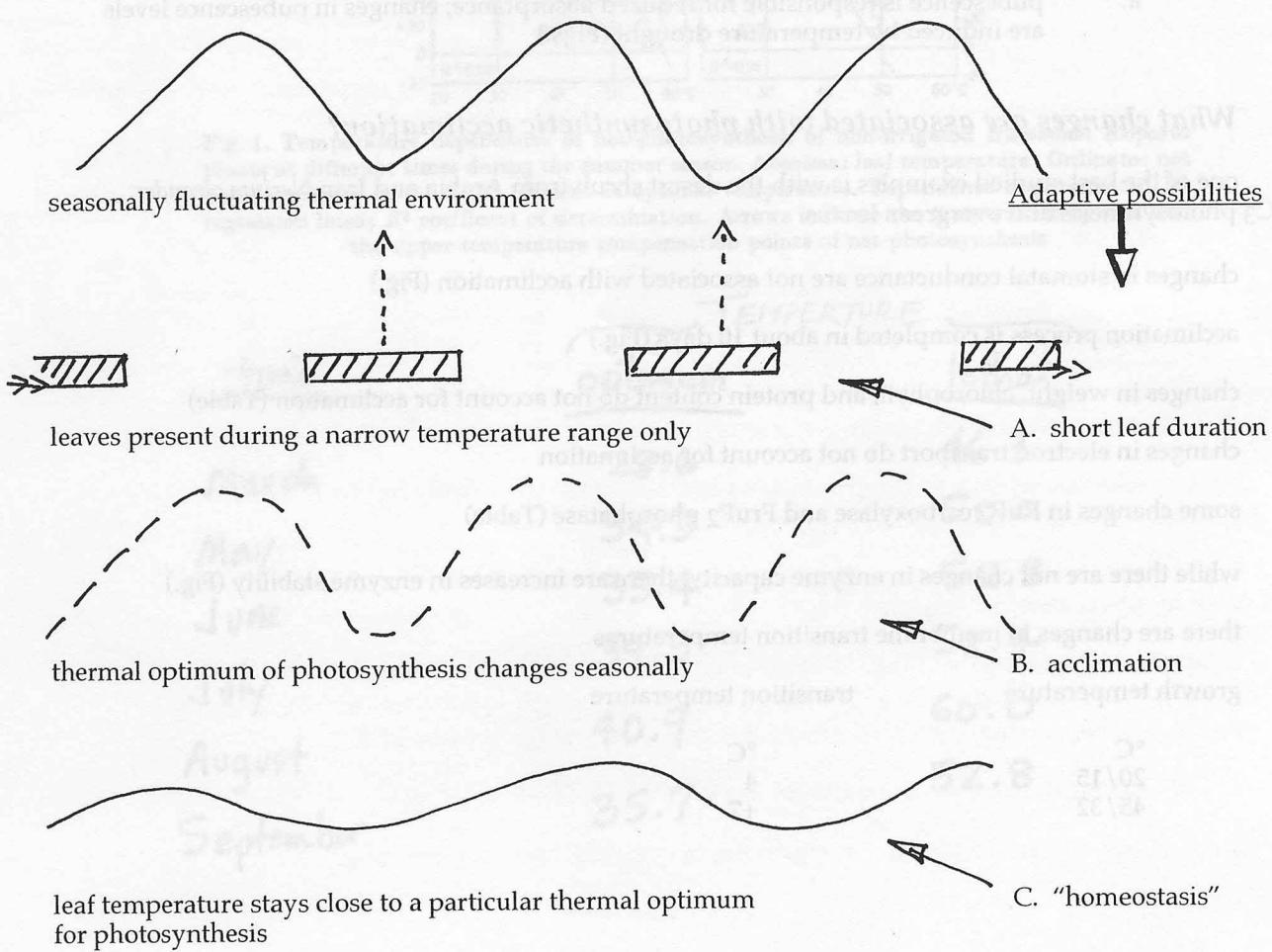
B. Intra- and inter-specific comparisons of species responses to cold - LOW TEMPERATURES

1. Root permeability and phase transitions in the root membrane is very important (Fig.)

2. This causes a change in total plant resistance and transpirational flux (Fig.)

3. Photosynthesis is depressed because of changes in plant water status (Fig.)

III. Adaptive possibilities to a change in thermal environment (Fig.)



- A. Short leaf duration
 - 1. leaves present for narrow temperature range only (some annuals and perennial herbs)
 - 2. no photosynthetic activity during other temperatures (as above)
 - B. Photosynthetic acclimation
 - 1. physiological and biochemical changes occur in leaf so that temperature optimum and upper temperature lethal limit change in concert with air temperatures
 - 2. leaves can be active year round if conditions permit
 - 3. *Pinus taeda* (loblolly pine of s.e. U.S.) has an evergreen leaf; C₃ photosynthesis (Fig.)
 - 4. *Hammada scoparia* (Negev Desert, Israel) with C₄ photosynthesis 12-15°C (Fig.)
 - C. "Homeostasis"
 - 1. physiological and biochemical changes do not occur so that temperature optimum and upper limit lethal temperature remain constant
 - 2. morphological and / or transpiration changes occur in leaves so that energy balance is modified and leaf temperature remains both constant and close to the thermal optimum of photosynthesis
 - 3. *Encelia farinosa* (Sonoran Desert) with C₃ photosynthesis changes leaf spectral characteristics and can achieve temperatures 10°C below air temperature (Fig.)
 - a. pubescence is responsible for reduced absorptance; changes in pubescence levels are induced by temperature drought (Figs.)

IV. What changes are associated with photosynthetic acclimation?

- A. one of the best studied examples is with the desert shrub from Arabia and Iran, *Nerium oleander*; with C₃ photosynthesis and evergreen leaves
 - B. changes in stomatal conductance are not associated with acclimation (Fig.)
 - C. acclimation process is completed in about 10 days (Fig.)
 - D. changes in weight, chlorophyll, and protein content do not account for acclimation (Table)
 - E. changes in electron transport do not account for acclimation
 - F. some changes in RuP₂ carboxylase and FruP₂ phosphatase (Table)
 - G. while there are not changes in enzyme capacity, there are increases in enzyme stability (Fig.)
 - H. there are changes in membrane transition temperatures

°C
20/15
45/32

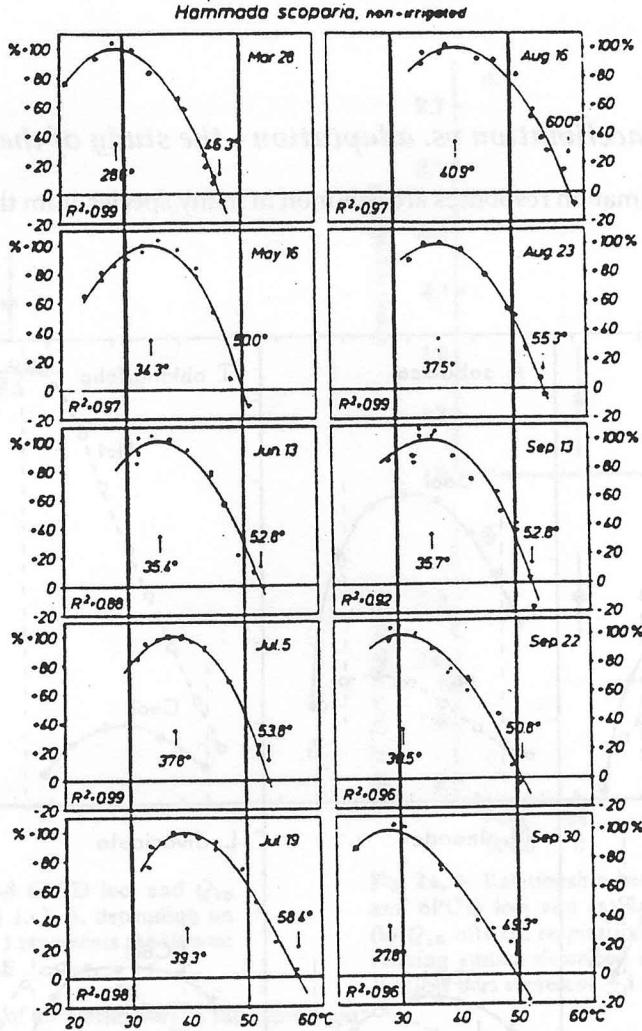


Fig. 1. Temperature dependence of net photosynthesis of non-irrigated *Hammada scoparia* plants at different times during the summer season. Abscissa: leaf temperature; Ordinate: net photosynthesis in % of CO_2 uptake at optimal temperature. Dependence approximated by regression lines; R^2 coefficient of determination. Arrows indicate the temperature optima and the upper temperature compensation points of net photosynthesis

<u>time</u>	<u>TEMPERATURE</u>	
	<u>optimum</u>	<u>lethal</u>
March	28.6	46.3
May	34.3	50.0
June	35.4	52.8
July	39.3	58.4
August	40.9	60.0
September	35.7	52.8

V. Photosynthetic acclimation vs. adaptation - the study of thermal ecotypes

- A. Photosynthetic acclimation responses are common in many species from thermally variable environments (Fig.)

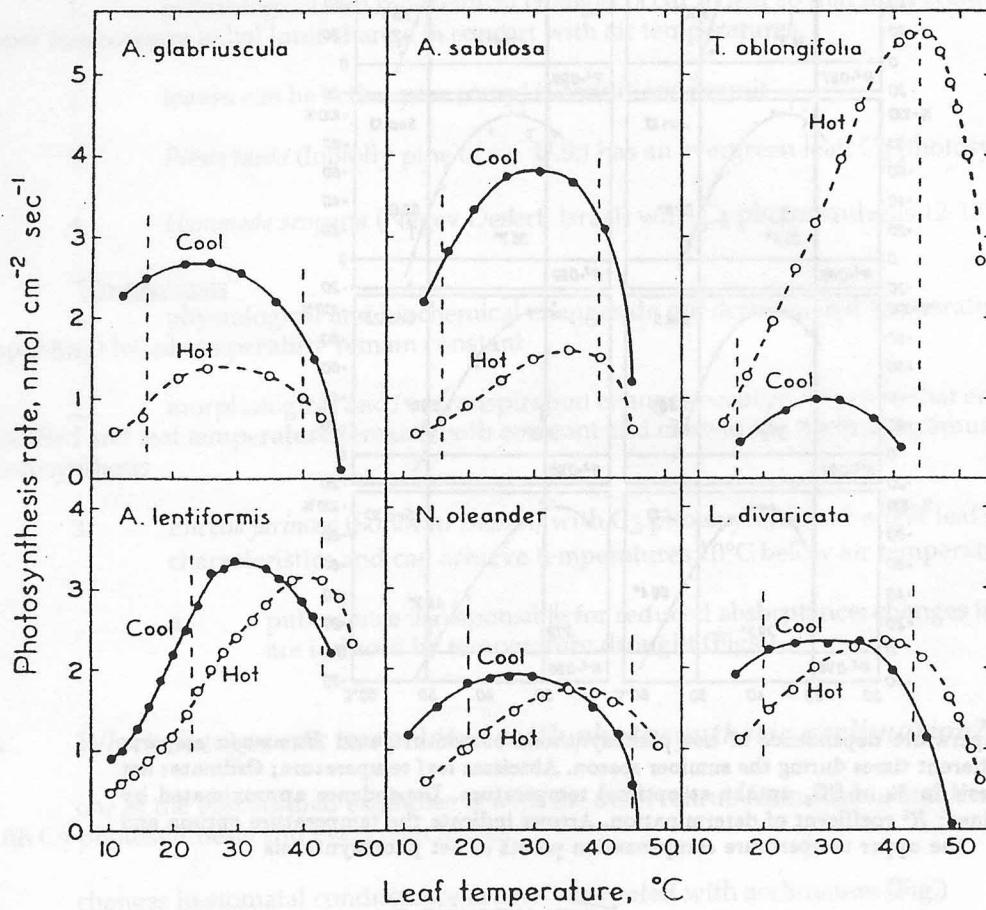


Figure 2 Effect of growth temperature regime on the rate and temperature dependence of light-saturated photosynthesis in normal air for a number of species native to habitats with contrasting thermal regimes. The vertical broken lines indicate the daytime temperatures of the "cool" and "hot" growth regimes for each species.

- B. Temperature optimum for photosynthesis can shift (Fig.) - example - *Eucalyptus pauciflora*
- C. Photosynthesis and dark respiration optima can both shift - genetically fixed within population of Arctic or Alpine origin (e.g. *Oxyria digyna*) - (Fig.)
- D. Populations can respond quite differently in their acclimation ability; e.g. *Atriplex lentiformis* with its desert and coastal clones (Figs.)
- E. Adaptive response can be due to shifts in enzyme activity, sensitivity, Q₁₀ (the increase in reaction rate that results from a 10° change (usually increased) in temperature - e.g. a Q₁₀ of 2 means that the reaction increased two-fold with a temperature increase of 10°)
1. Malate dehydrogenase ecotypes in *Typha latifolia* (Fig.)
 2. Q₁₀ of dark respiration in genotypes of ryegrass, *Lolium perenne* (Fig.)

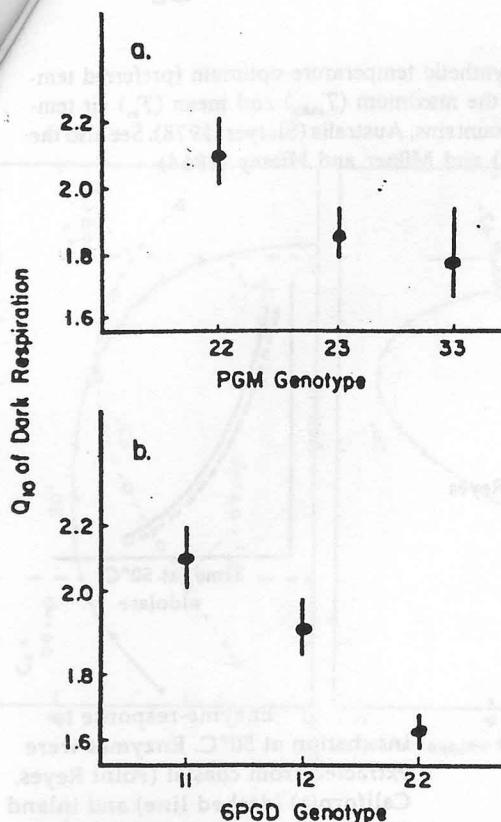


Fig. 1a, b. Relationship between PGM and 6PGD loci and Q_{10} of dark respiration. Genotypes are named 1, 2, 3, depending on their mobilities on the starch gel. Genotype 1 represents the slowest moving band. Vertical bars represent ± 1 SE

Table 1. Genotypic and allelic frequencies of all plants used in the experiment

Locus	Genotypic Frequencies								N	$F(1) \pm S.E.$	$F(2) \pm S.E.$	$F(3) \pm S.E.$	$F(4) \pm S.E.$	X^2	
	11	12	22	13	23	33	24	34							
Pgm	-	-	33	-	23	4	-	-	60	-	0.74 ± 0.040	0.26 ± 0.040	-	0.00	
Per	2	22	36	-	-	-	-	-	60	0.22 ± 0.038	0.78 ± 0.038	-	-	0.15	
6Pgd	37	18	5	-	-	-	-	-	60	0.77 ± 0.039	0.23 ± 0.039	-	-	0.65	
Udp	0	7	39	1	12	1	-	-	60	0.38 ± 0.044	0.18 ± 0.035	0.44 ± 0.045	-	0.00	
Pgi	-	-	-	-	6	33	5	15	1	60	-	0.33 ± 0.043	0.26 ± 0.040	0.42 ± 0.045	0.32

Note: X^2 tests the fit of observed to expected frequencies. $F(1)$, $F(2)$, $F(3)$ and $F(4)$ refer to allelic frequencies 1 through 4. SE = standard error

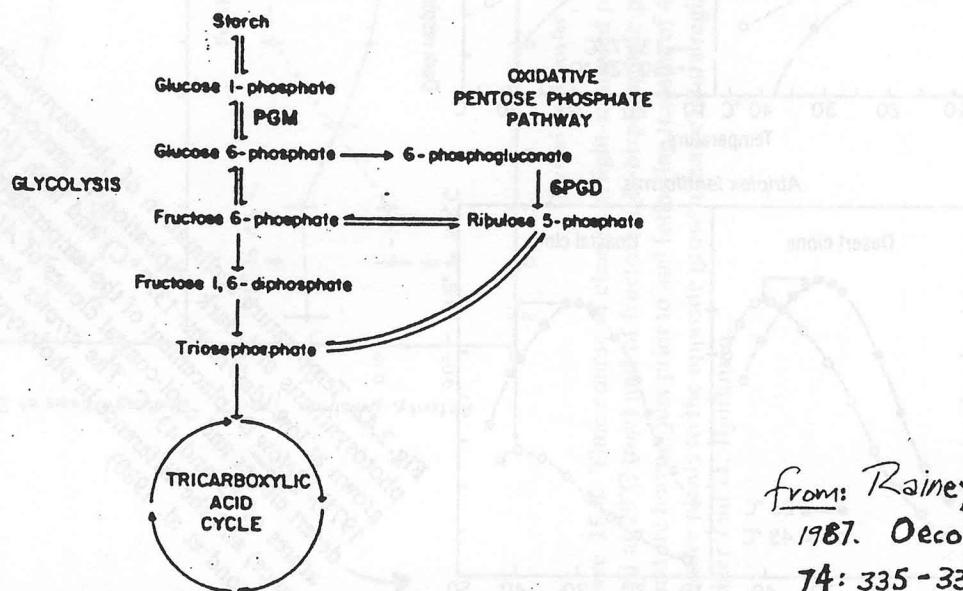


Fig. 3. A summary of the glycolytic and oxidative pentose phosphate pathways showing the positions of PGM and 6PGD

from: Rainey et al.
1987. Oecologia
74: 335 - 338

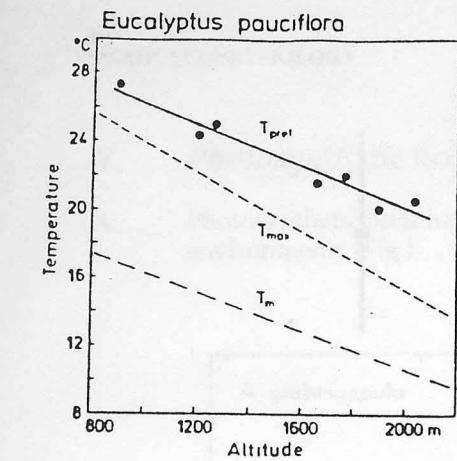


Fig. Altitudinal gradients of the photosynthetic temperature optimum (preferred temperature T_{pre}) of *Eucalyptus pauciflora*, and the maximum (T_{max}) and mean (T_m) air temperature of the warmest month in the Snowy Mountains, Australia (Slatyer, 1978). See also the classical studies of Pisek and Winkler (1959) and Milner and Hiesey (1964)

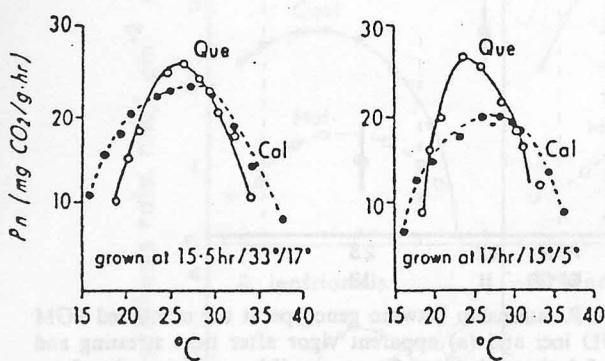
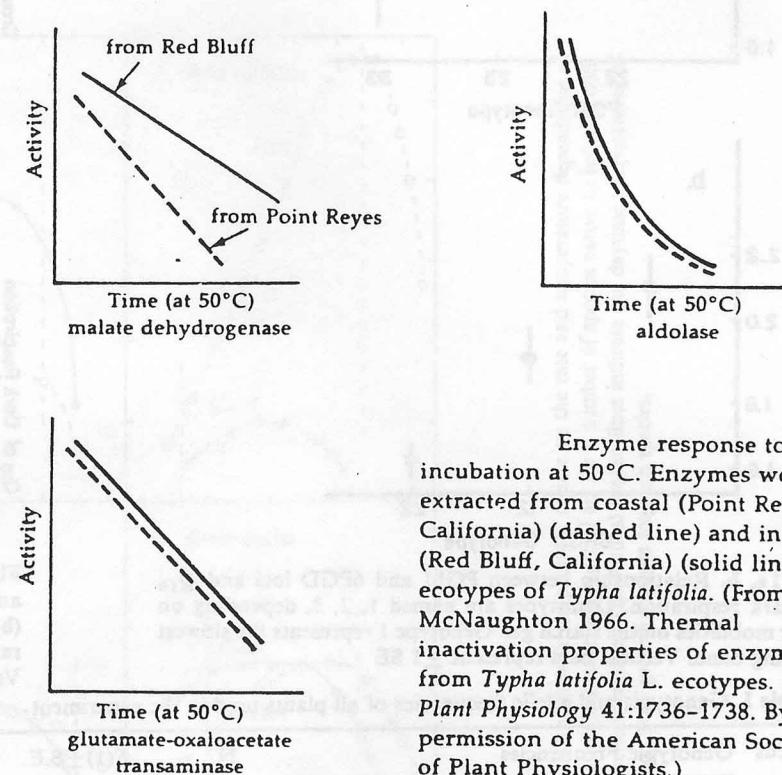
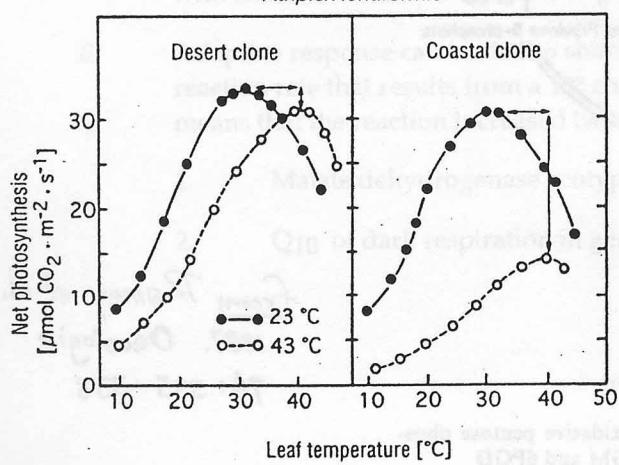
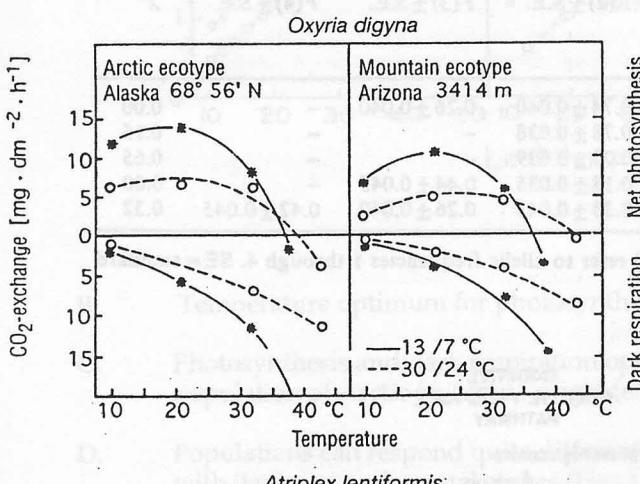


Fig. 4. Relationship between air temperature and net photosynthesis of leaves from *T. latifolia* ecotypes.



Enzyme response to incubation at 50°C. Enzymes were extracted from coastal (Point Reyes, California) (dashed line) and inland (Red Bluff, California) (solid line) ecotypes of *Typha latifolia*. (From McNaughton 1966. Thermal inactivation properties of enzymes from *Typha latifolia* L. ecotypes. *Plant Physiology* 41:1736-1738. By permission of the American Society of Plant Physiologists.)

Fig. 2.42. Temperature acclimation of photosynthesis in arctic and mountain ecotypes of *Oxyria digyna* grown at low (day/night: 13/7 °C) and high (30/24 °C) temperatures. (After Billings et al. 1971). Below Displacement of the temperature-dependence curves for photosynthesis of hot-desert clones and cool-coastal clones for *Atriplex lentiformis* (C_3) grown at daytime temperatures of 23 and 43 °C. The arrows denote the amplitude of acclimation (vertical distance). (After Pearcy, from Osmond et al. 1980)

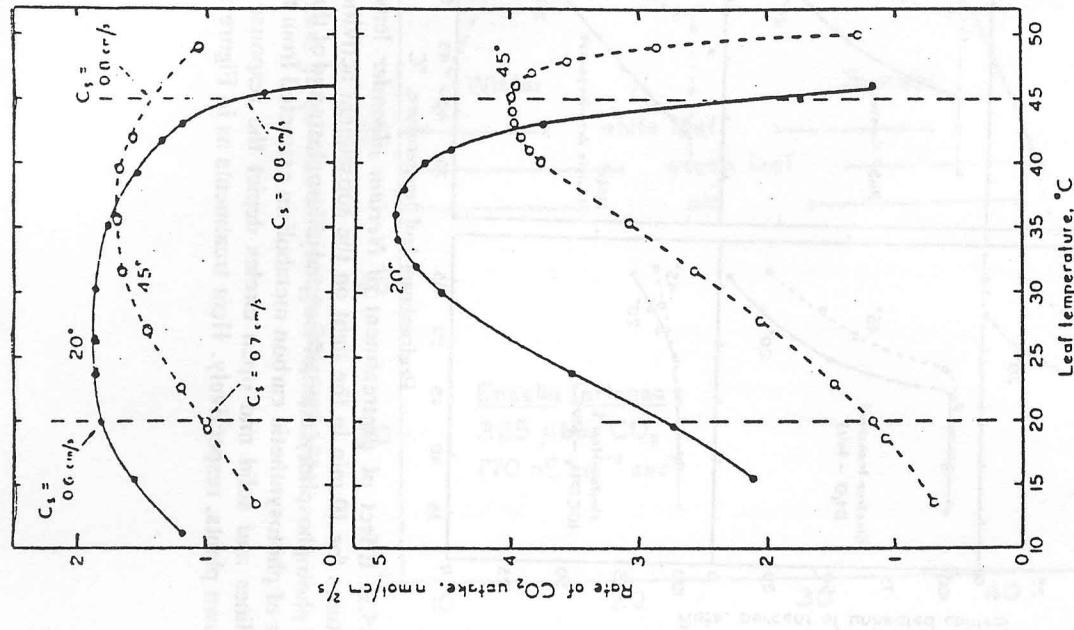


Figure 15.7. Temperature dependence of light-saturated CO_2 uptake for *Nerium oleander*, grown at two contrasting temperature regimes (20°C day/ 15°C night and 45°C day/ 32°C night). Measurements were made in normal air (top) $330 \mu\text{l/l}$ CO_2 , 21% v/v oxygen, and at high CO_2 concentration (bottom) $750 \mu\text{l/l}$ CO_2 , 20% v/v oxygen. Also shown are the stomatal conductances C_s measured at the two daytime growth temperatures. These temperatures are indicated by the broken vertical lines. Data from Ref. 15.

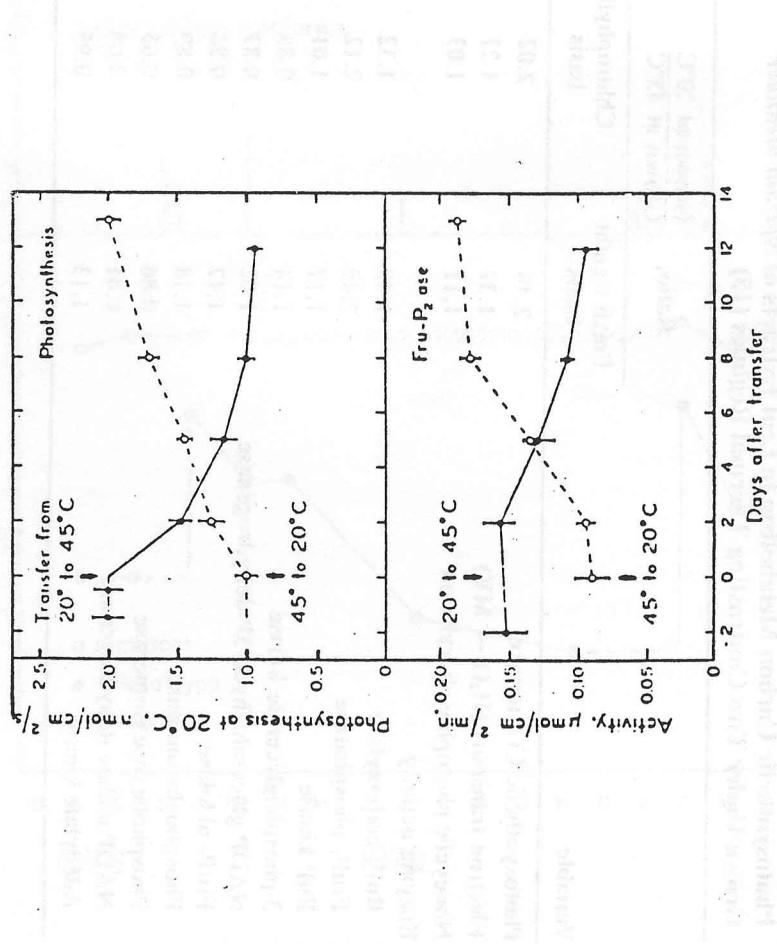


Figure 15.8. Time course of change in light-saturated photosynthetic capacity, measured at 20°C (top) and of fructose-1,6-bisphosphate phosphatase activity (bottom) in mature leaves, just prior to and following transfer of 45°C - and 20°C -grown *Nerium oleander* plants to the opposite growth temperature regimes. Unpublished data of M. Badger and O. Björkman.

Bottom left:
Photosynth (μmol/CJ^-2)
Top left:
Fru-P2 (μmol/catalyst hr^-1)

Bottom right:
Leaf conductance (mmol m^-2 s^-1)
Top right:
Stomatal conductance (μmol m^-2 s^-1)

Table 15.2. Leaf Specific Weights and Chlorophyll and Protein Contents of *Nerium oleander* Leaves, Grown Under Two Contrasting Thermal Regimes (15)

Variable	A: Grown at 20°C	B: Grown at 45°C	A/B
Fresh weight (mg/cm ²)	44.2	45.8	0.97
Dry weight (mg/cm ²)	12.6	15.4	0.82
Chlorophyll <i>a</i> + <i>b</i> (mg/cm ²)	0.076	0.065	1.19
Total protein (mg/cm ²)	1.41	1.65	0.85
Soluble protein (mg/cm ²)	0.67	0.64	1.05
Insoluble protein (mg/cm ²)	0.74	0.94	0.79

Table 15.3. Comparison of Photosynthetic Capacity at 20°C of Intact Leaves, Photosynthetic Electron Transport, and Photophosphorylation Capacities of Isolated Chloroplasts, and Activities of Enzymes of Photosynthetic Carbon Metabolism in Leaf Extracts of *Nerium oleander* Grown Under Two Contrasting Thermal Regimes (15)

Variable	Grown at 20°C Ratio, Grown at 45°C	Chlorophyll basis
Photosynthetic CO ₂ uptake	2.40	2.02
Electron transport (H ₂ O → MV)	1.37	1.27
Noncyclic photophosphorylation	1.11	1.03
Enzyme activity		
RuP ₂ carboxylase	1.49	1.32
FruP ₂ phosphatase	2.46	2.12
RuP kinase	1.17	1.01
3-phosphoglycerate kinase	1.14	0.88
NADP glyceraldehyde-3P-dehydrogenase	1.02	0.87
FruP ₂ aldolase	1.17	0.96
Phosphoglucomutase	1.18	0.89
Phosphoenolpyruvate isomerase	0.86	0.65
NADP malate dehydrogenase	0.81	0.63
Adenylyl kinase	1.13	0.95

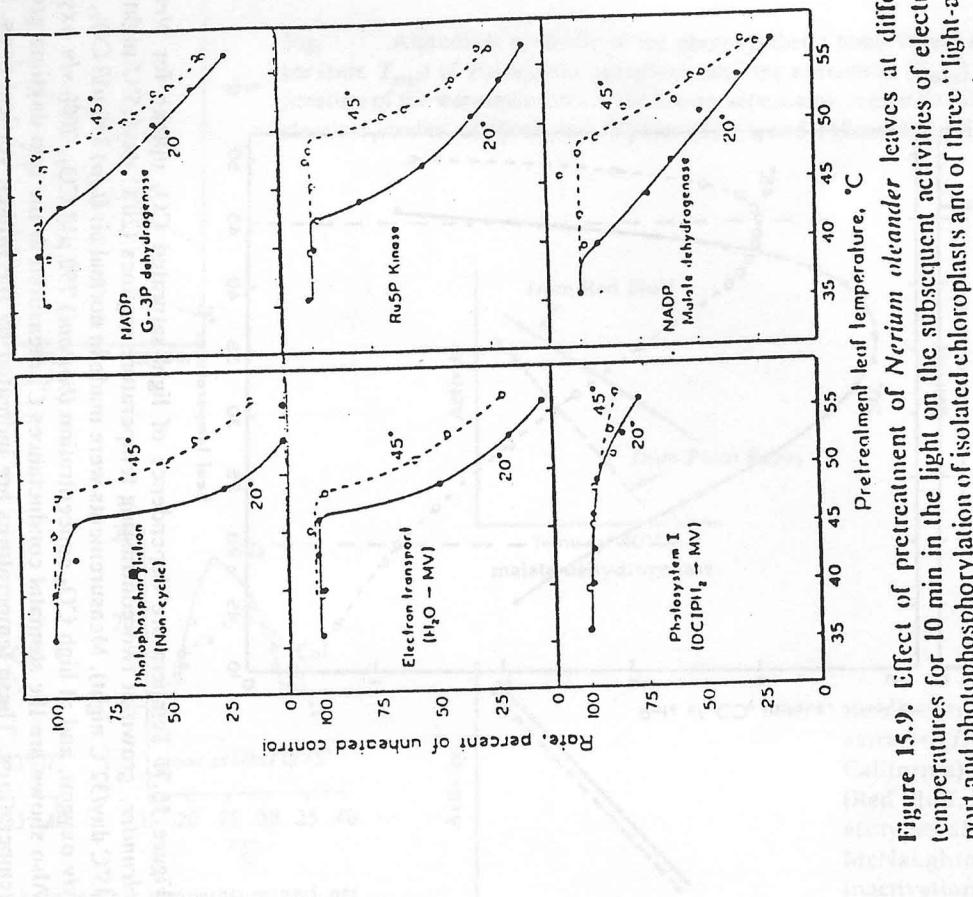
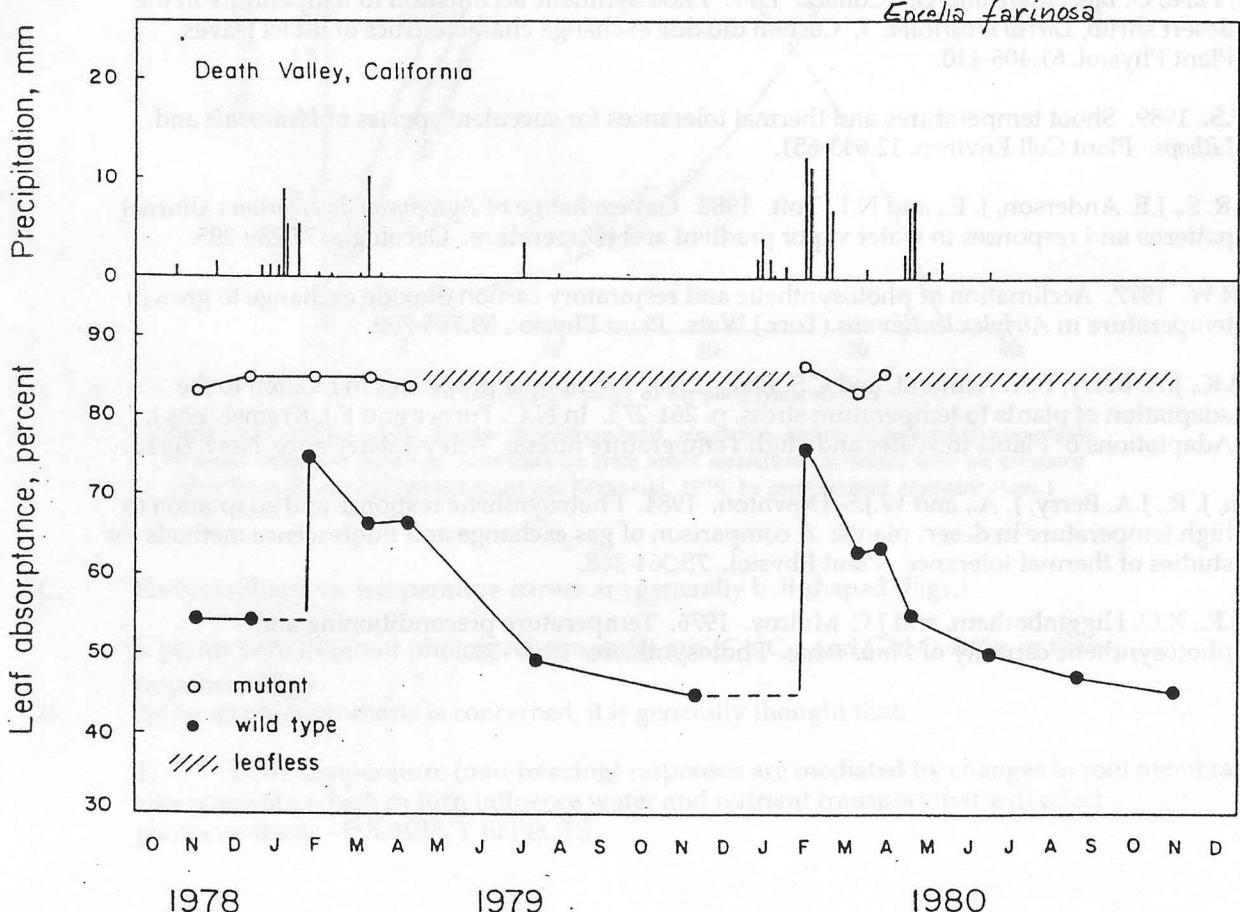
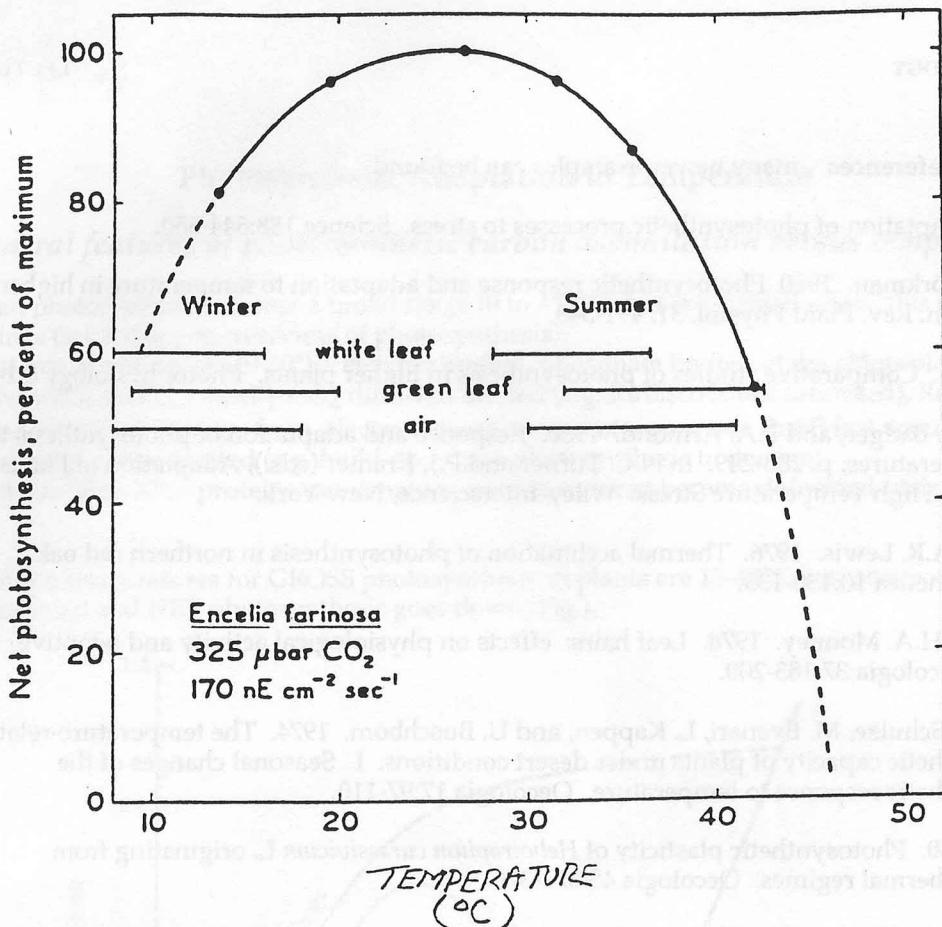


Figure 15.9. Effect of pretreatment of *Nerium oleander* leaves at different temperatures for 10 min in the light on the subsequent activities of electron transport and photophosphorylation of isolated chloroplasts and of three "light-activated" enzymes of photosynthetic carbon metabolism extracted from the leaves. Solid broken lines and solid and open circles depict the response of 20°C-grown 45°C-grown plants, respectively. Heat treatments as in Figure 15.5. From Ref.



Some "Classic" References - many newer examples can be found

- Berry, J. 1975. Adaptation of photosynthetic processes to stress. *Science* 188:644-650.
- Berry, J., and O. Björkman. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Ann. Rev. Plant Physiol.* 31: 491-543.
- Björkman, O. 1973. Comparative studies of photosynthesis in higher plants. *Photophysiology* 8:1-63.
- Björkman, O., M.R. Badger, and P.A. Armond. 1980. Response and adaptation of photosynthesis to high temperatures, p. 233-249. In N.C. Turner and P.J. Kramer (eds.), *Adaptation of Plants to Water and High Temperature Stress*. Wiley-Interscience, New York.
- Chabot, B.F., and A.R. Lewis. 1976. Thermal acclimation of photosynthesis in northern red oak. *Photosynthetica* 10:130-135.
- Ehleringer, J., and H.A. Mooney. 1978. Leaf hairs: effects on physiological activity and adaptive value to a desert shrub. *Oecologia* 37:183-200.
- Lange, O.L., E.-D. Schulze, M. Evenari, L. Kappen, and U. Buschbom. 1974. The temperature-related photosynthetic capacity of plants under desert conditions. I. Seasonal changes of the photosynthetic response to temperature. *Oecologia* 17:97-110.
- Mooney, H.A. 1980. Photosynthetic plasticity of *Heliotropium curassivicum* L. originating from differing thermal regimes. *Oecologia* 45:372-376.
- Mooney, H.A. and M. West. 1964. Photosynthetic acclimation of plants of diverse origin. *Amer. J. Bot.* 51:825-827.
- Mooney, H.A., O. Björkman, and G.J. Collatz. 1977. Photosynthetic acclimation to temperature in the desert shrub, *Larrea divaricata*. I. Carbon dioxide exchange characteristics of intact leaves. *Plant Physiol.* 61:406-410.
- Nobel, P.S. 1989. Shoot temperatures and thermal tolerances for succulent species of *Haworthia* and *Lithops*. *Plant Cell Environ.* 12:643-651.
- Nowak, R. S., J.E. Anderson, J. E., and N.L. Toft. 1988. Gas exchange of *Agropyron desertorum* : diurnal patterns and responses to water vapor gradient and temperature. *Oecologia* 77:289-295.
- Pearcy, R.W. 1977. Acclimation of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentiformis* (Torr.) Wats. *Plant Physiol.* 59:795-799.
- Raison, J.K., J.A. Berry, P.A. Armond, and C.S. Pike. 1980. Membrane properties in relation to the adaptation of plants to temperature stress, p. 261-273. In N.C. Turner and P.J. Kramer (eds.), *Adaptations of Plants to Water and High Temperature Stress*. Wiley-Interscience, New York.
- Seemann, J. R., J.A. Berry, J. A., and W.J.S. Downton. 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.
- Strain, B.R., K.O. Higginbotham, and J.C. Mulroy. 1976. Temperature preconditioning and photosynthetic capacity of *Pinus taeda*. *Photosynthetica* 10:47-53.