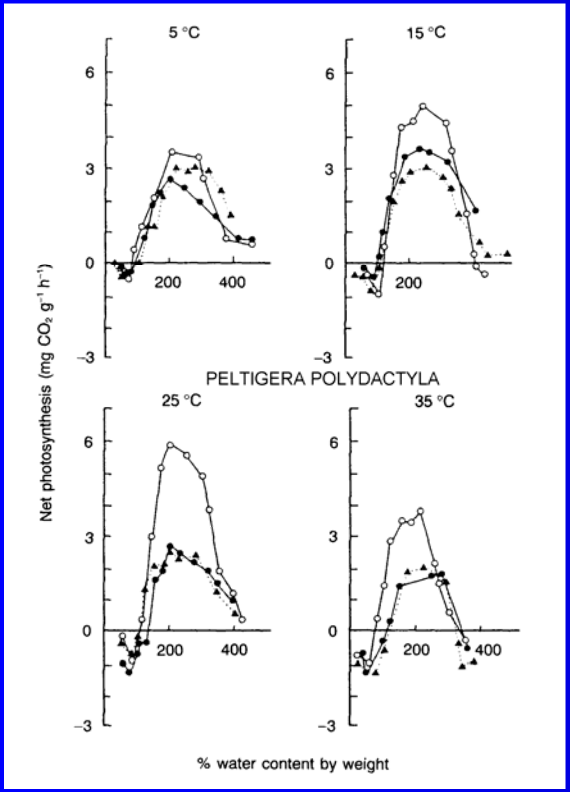
# Lichen Physiology I



# Overview of Topics

- Photosynthesis and Respiration
  - Including water relations, productivity, desiccation, carbon transfer, growth and lichenometry
- Nitrogen Metabolism
- Nutrients and Mineral Cycling

# Photosynthesis/Respiration

- Because lichens are dominant members of some ecosystems (coastal deserts and polar areas), understanding this aspect of **primary productivity** is important to understanding ecosystem functioning.
- These processes are "measured" by determining rates of gas exchange ($CO_2$ uptake or $O_2$ release)

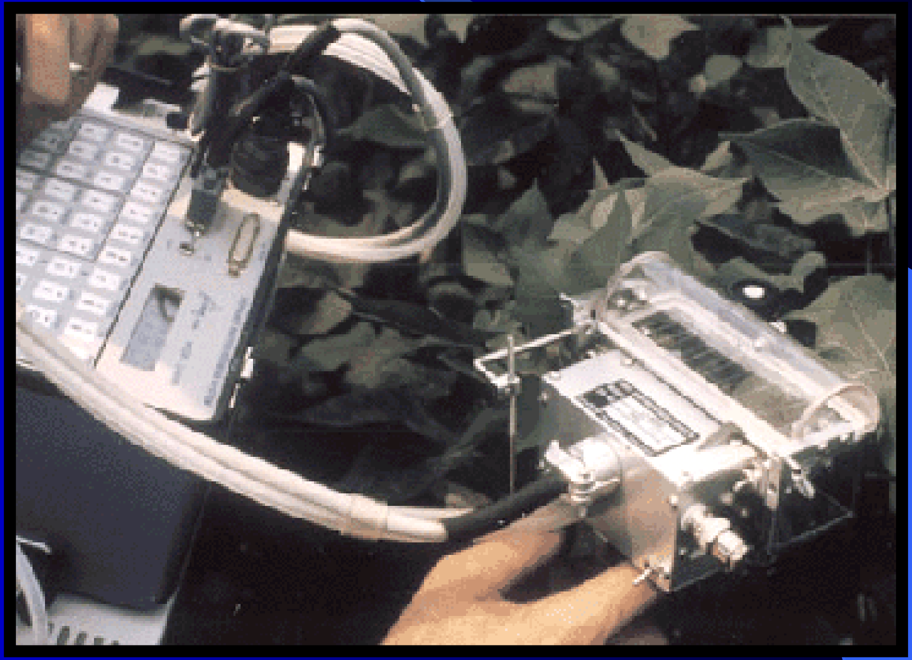
# Measuring Gas Exchange

- **Photosynthesis** as either $CO_2$ uptake or $O_2$ release
- **Dark respiration** as either $O_2$ uptake or $CO_2$ release
- Some investigators have used $^{14}CO_2$ assimilation into carbohydrate, but this lab technique does not usually approximate true environmental conditions.

# Measuring Gas Exchange (cont.)

- The preferred field technique, however, is to use an **infrared gas analysis system** (which can be portable)
  - In a controlled open system, atmospheric $CO_2$ depletion is measured continuously in a "flow through system" or…
  - In a closed cuvette, initial and final measurements are taken after a set time period

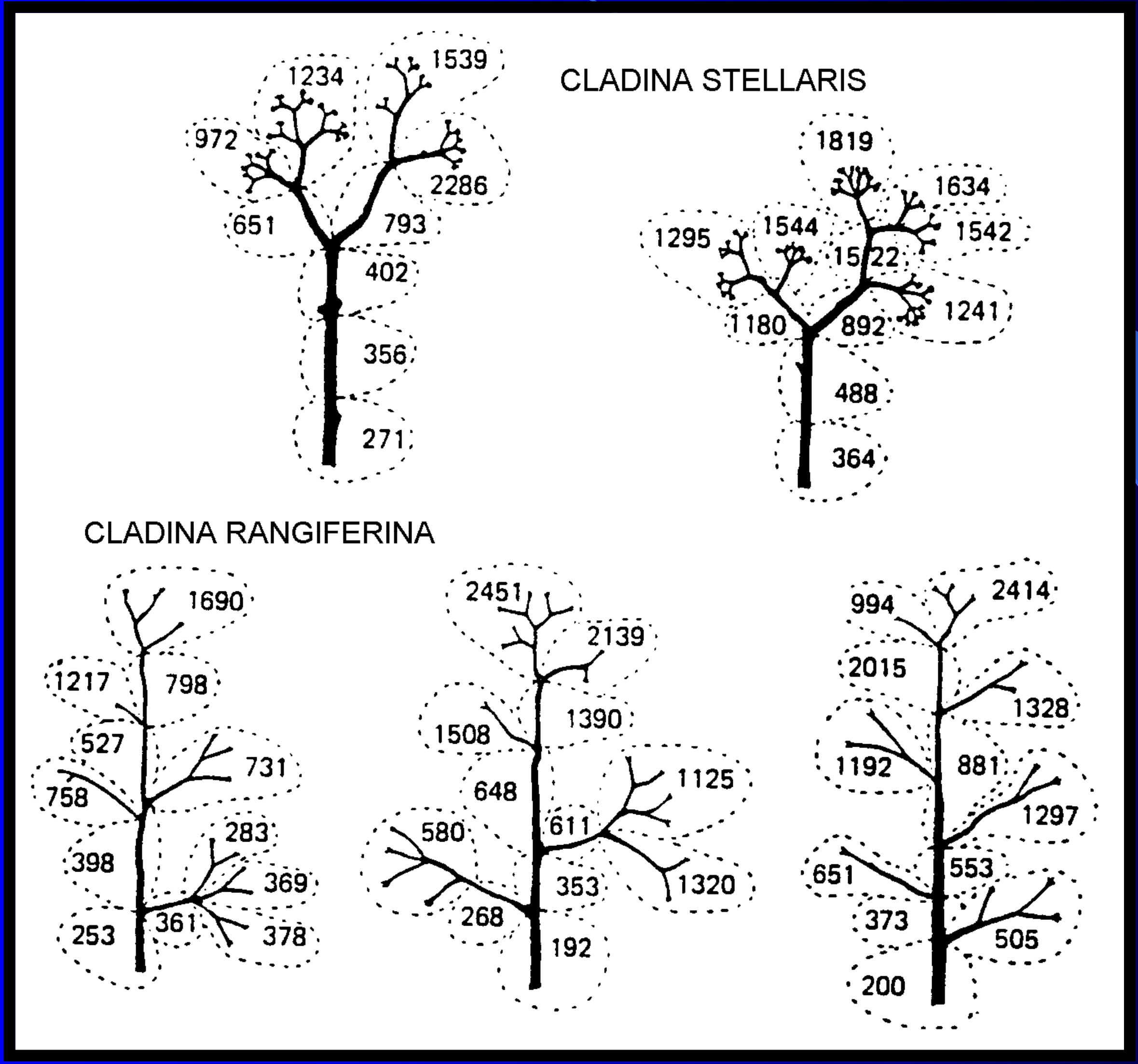
# $CO_2$ Gas Analyzers



# $CO_2$ Exchange Variability

- Do all portions of the thallus photosynthesize at the same rate?
- How does the rate of photosynthesis compare to measurements in higher plants?

# Photosynthesis in *Cladina*



# Comparisons

- Lower rates are reported in lichens, however ……
- Most published results used the whole lichen thallus and results are expressed as assimilation of $CO_2$ **per unit dry weight**
- In higher plants, it is usually expressed as assimilation **per unit leaf surface area**
- Erroneous comparison: like putting the whole tree in an analysis chamber!

# Environmental Influences on Gas Exchange

- Thallus water content
- Temperature
- Light
- $CO_2$ levels

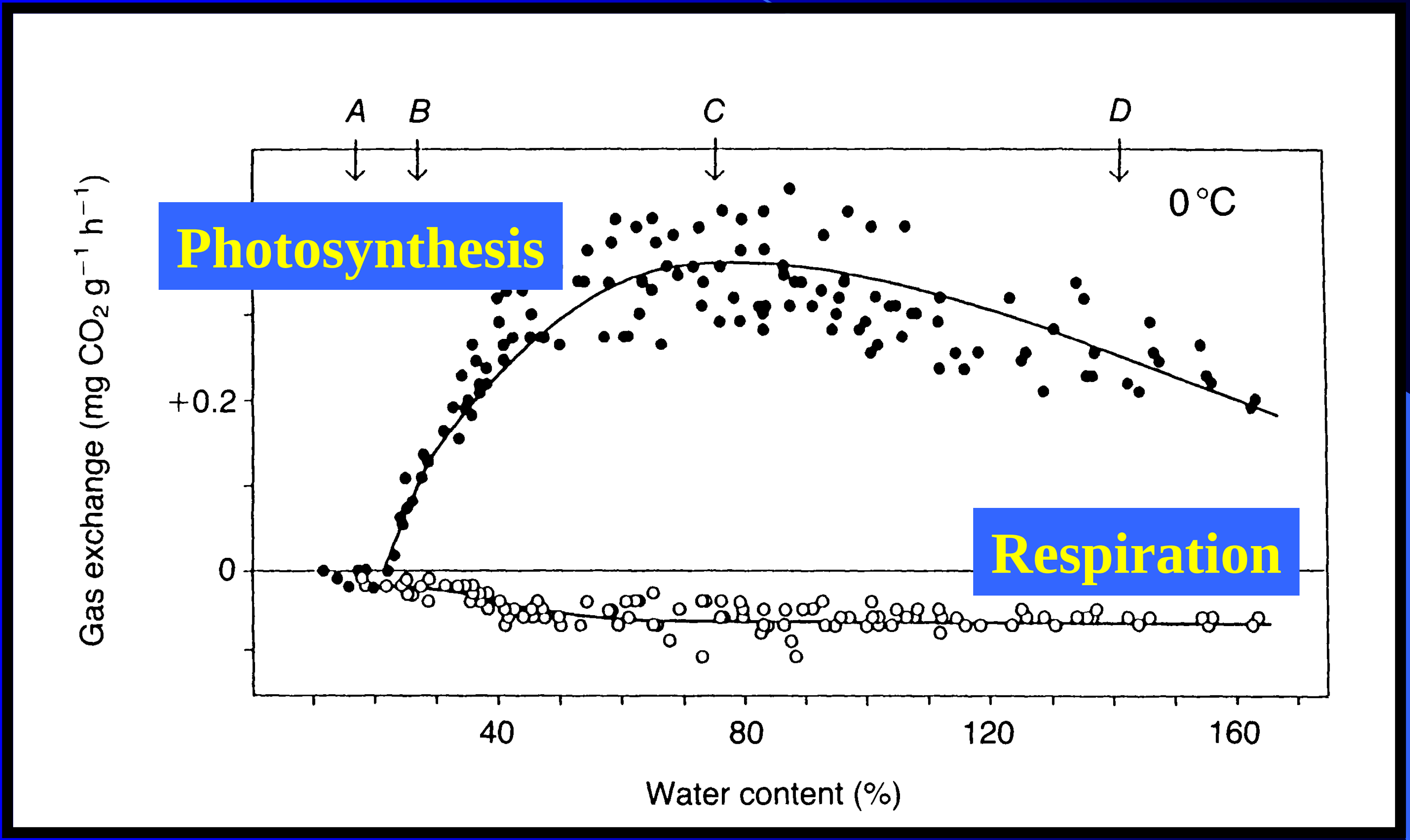
# Thallus Water Content

- Lichen thalli can exhibit a wide range of thallus water content:
  - Normal, air dry thalli are typically less than 15-30% (of oven-dry weight)
  - However, water absorption can go as high as 250-400% with green algal partners and 600-2000% with cyanobionts

# Water Content & Gas Exchange

- As water content increases, initial gas exchange is primarily $CO_2$ **release** as a result of cellular respiration (A)
- At approximately 22%, the net $CO_2$ loss and gain are equal (B). This is known as the **WATER COMPSENSATION POINT.**
- Subsequent uptake allows increasing photosynthetic activity

# Effect of $H_20$ Content on $CO_2$ Uptake



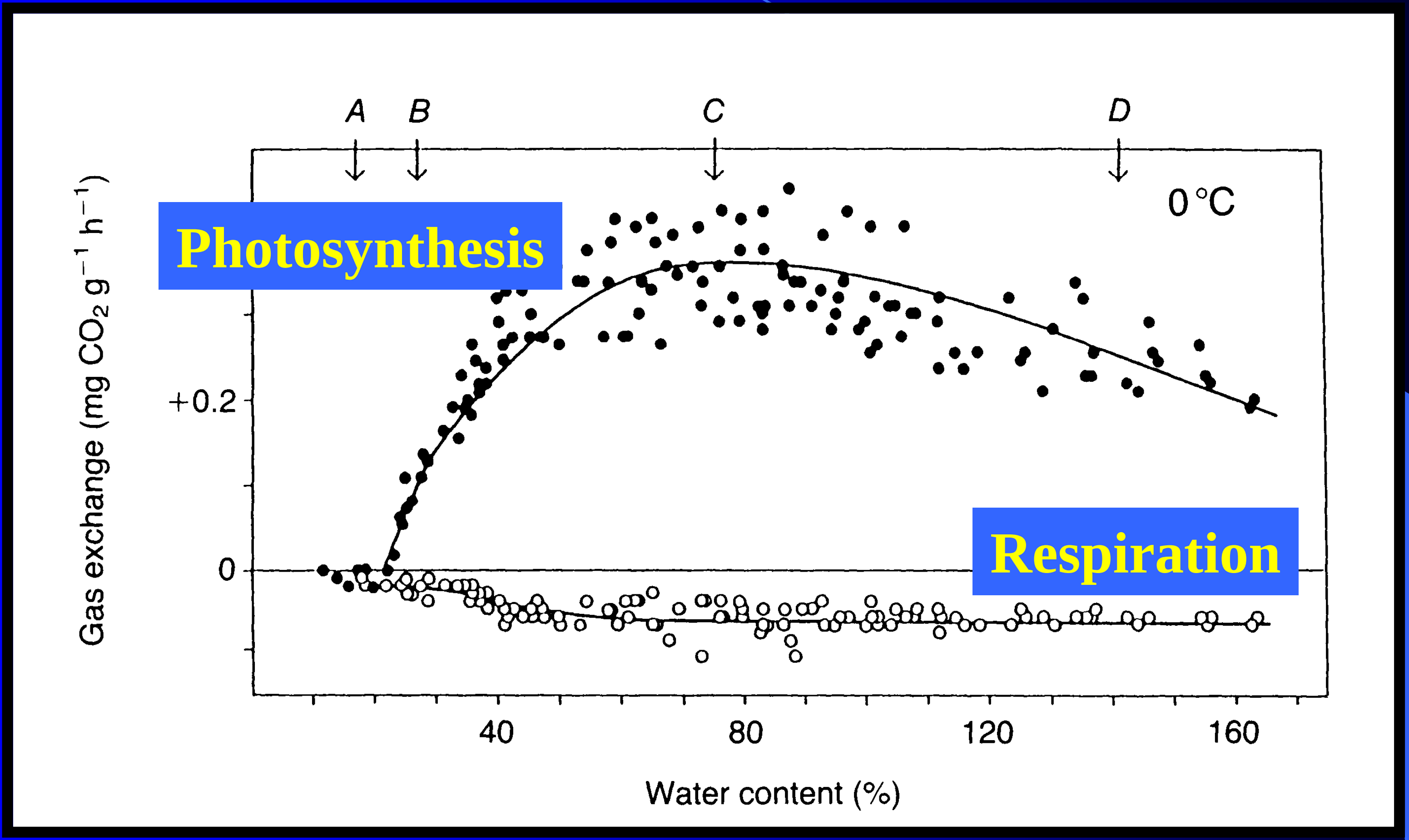
# Water Content & Gas Exchange (Cont.)

- Photosynthetic activity is optimal at 70-150% water content (phycobionts) and 300-600% for cyanobionts (C)
- Afterwards, at higher water contents, the photosynthetic rate declines, especially at higher temperatures primarily because of decreased solubility of $CO_2$ (D)

# Water Content & Gas Exchange (Cont.)

- Respiration exhibits a generally constant relationship with maximum values at approximately the same water content level as maximum photosynthesis
- Higher water contents, however, do not significantly effect dark respiration
- However, sudden reactivation from a desiccated state shows a different pattern (discussed under “desiccation”)

# Effect of $H_20$ Content on $CO_2$ Uptake



# Why this pattern?

- Two major phenomena are probably involved:
  - (a) **Reactivation of metabolic processes** associated with photosynthesis, and …
  - (b) **Increasing resistance to $CO_2$ inward flux** with higher water contents

# Reactivation of Metabolism

- Air dry lichens and photobionts can withstand water contents far lower than vascular plants (they would be permanently wilted)
  - The lichen polyol and polyamine concentrations protect conformational integrity of the lichen proteins during desiccation
- Full reactivation, as a result, takes time **and energy** (thus $CO_2$ release at first)

# $CO_2$ Flux Resistance

- Resistance to $CO_2$ uptake is greater when the $CO_2$ must move through water than it is when it moves through air
- At intermediate levels (optimum), the saturation level is sufficient for metabolic activity, but the thallus still has “air channels” through which $CO_2$ movement is possible

# Water Uptake Processes

- Lichens obtain water from a variety of sources: **precipitation**, **fog**, **dew**, and **elevated humidities**
- All are capable of activating gas exchange for photosynthesis and growth

# Water Uptake Processes (cont.)

- Uptake best in lichens with green photobionts with **lower temperatures**, **high relative humidity**
- This uptake is enhanced by high polyol solute concentrations (hypertonic)
- Cyanobionts do not become turgid (or begin photosynthesis) without **liquid water uptake**. Therefore, these species tend to be more common in moist environments.

# Effects of Temperature

- Lichens are inhabitants of some of the hottest (and coldest) places on earth
- Microhabitat differences can be extreme
  - Sunny rock surface (enormous daily fluctuation)
  - Sheltered overhangs (reflects primarily ambient temperature variation)

# Temperature Tolerance (Heat)

- **Dry thalli are highly resistant**
  - When wet, heat tolerance may decline by 40-50ºC
  - Heat tolerance decreases with length of exposure
  - Some lichens can regain normal photosynthesis after immersion as low as -196ºC for several days (if thawing is not too rapid)

# Temperature Tolerance (Cold)

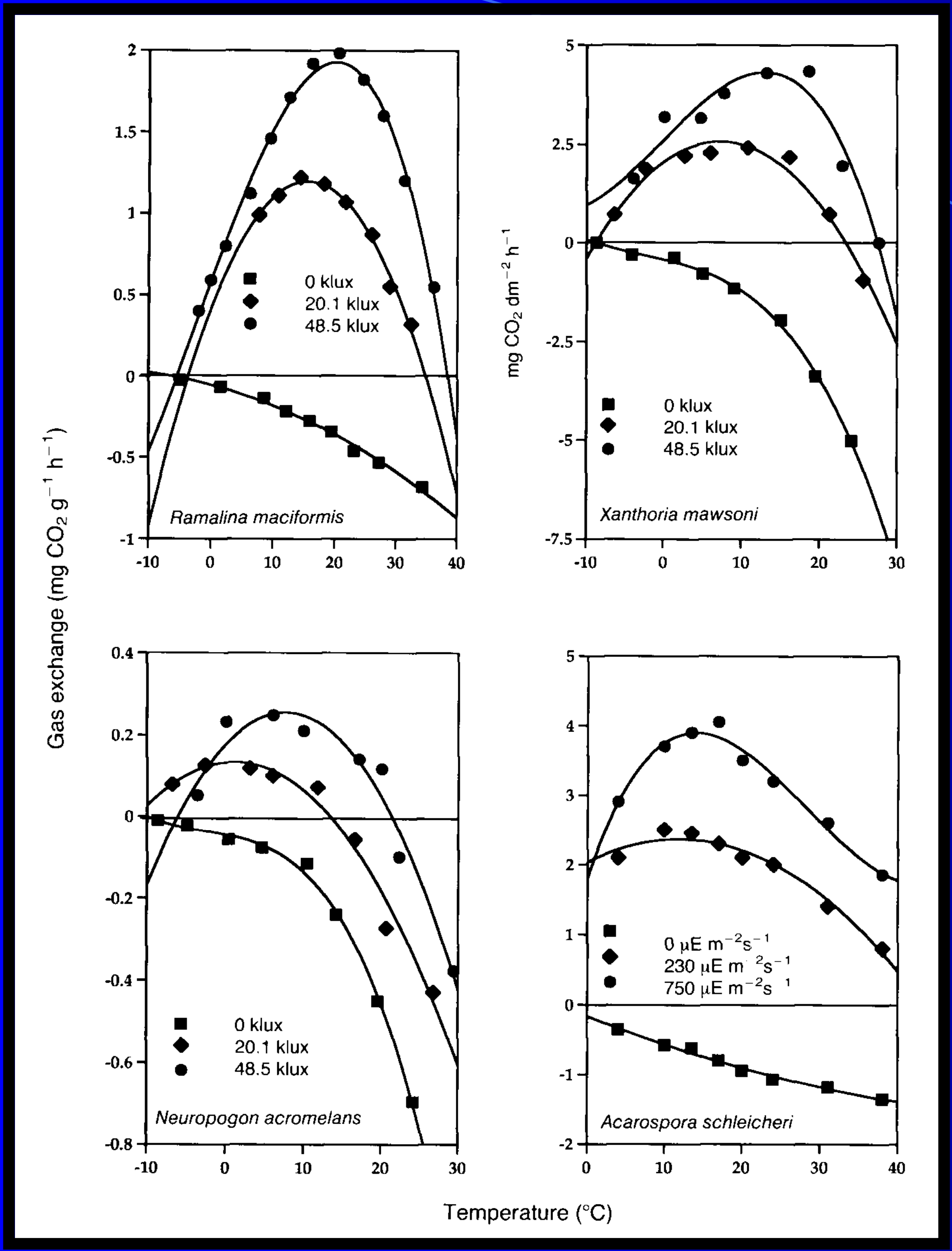
- **Photobiont cells are most sensitive**
- Those adapted to warmer environments are generally less tolerant

# Mechanisms of Tolerance

- High concentrations of polyols probably serve as “protectants” for heat/cold sensitive proteins
- The polyols also reduce the likelihood of ice crystal formation and, more importantly, desiccation injury

# Temperature Effects on Gas Exchange

- Lichens from different regions have distinct **temperature optima** for photosynthesis, although these optima are not widely divergent.
  - Desert species do best in winter or in early morning hours
  - Arctic/Antarctic taxa do best in summer when temperatures are higher



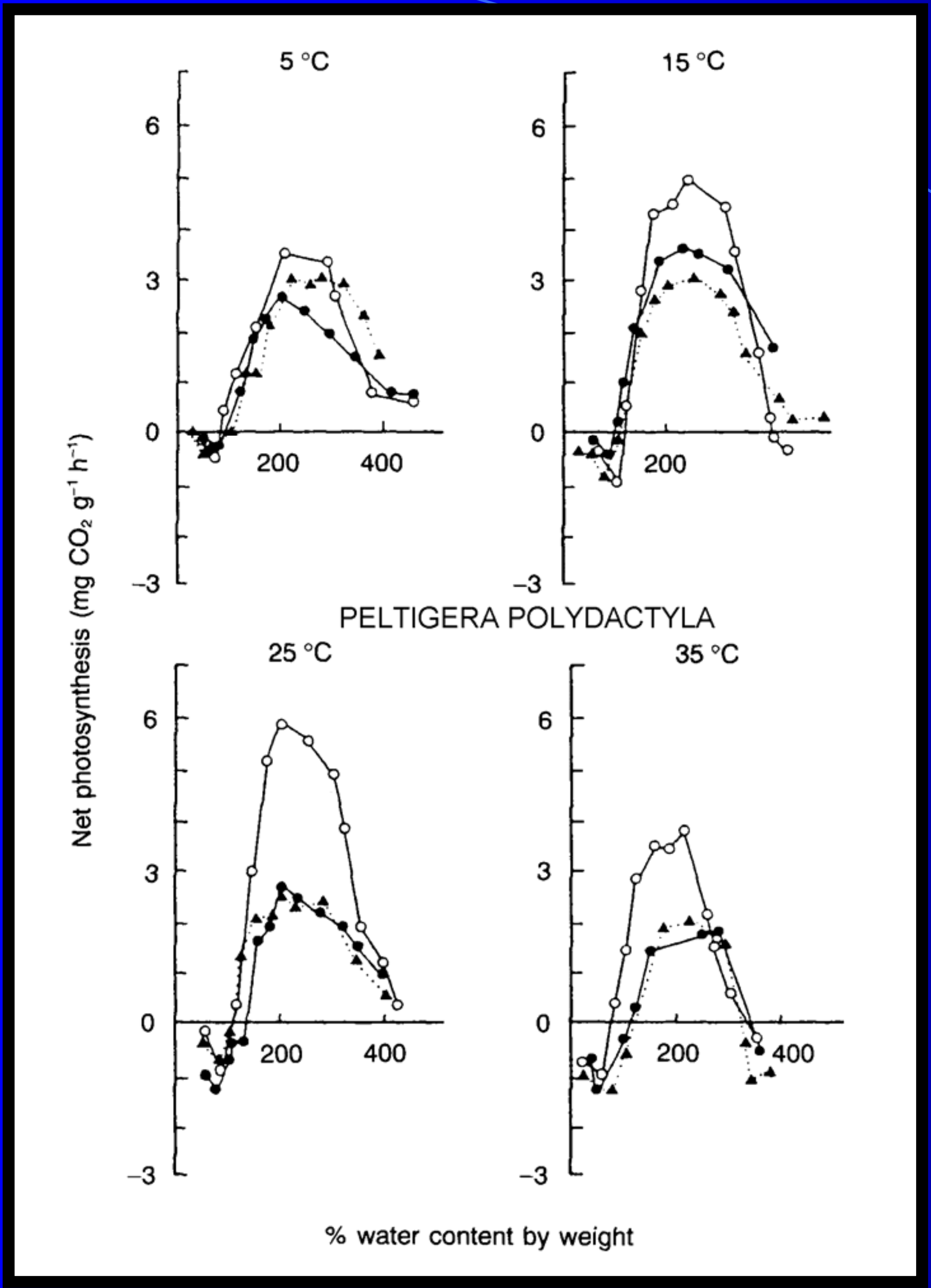

# Effect of **temperature** on net photosynthesis and dark respiration at different light levels.

TOP ROW: taxa from the **desert**

BOTTOM ROW: taxa from **Antarctica**

# Temperature Effects on Gas Exchange (cont.)

  - Some Antarctic taxa are actually able to sustain carbon gain at temperatures below freezing
- Some lichens show “seasonal changes” or shifts in photosynthetic rates
  - This variation is often called “**acclimation**” or “**alternations in photosynthetic capacity**”
  - See next slide ……………..

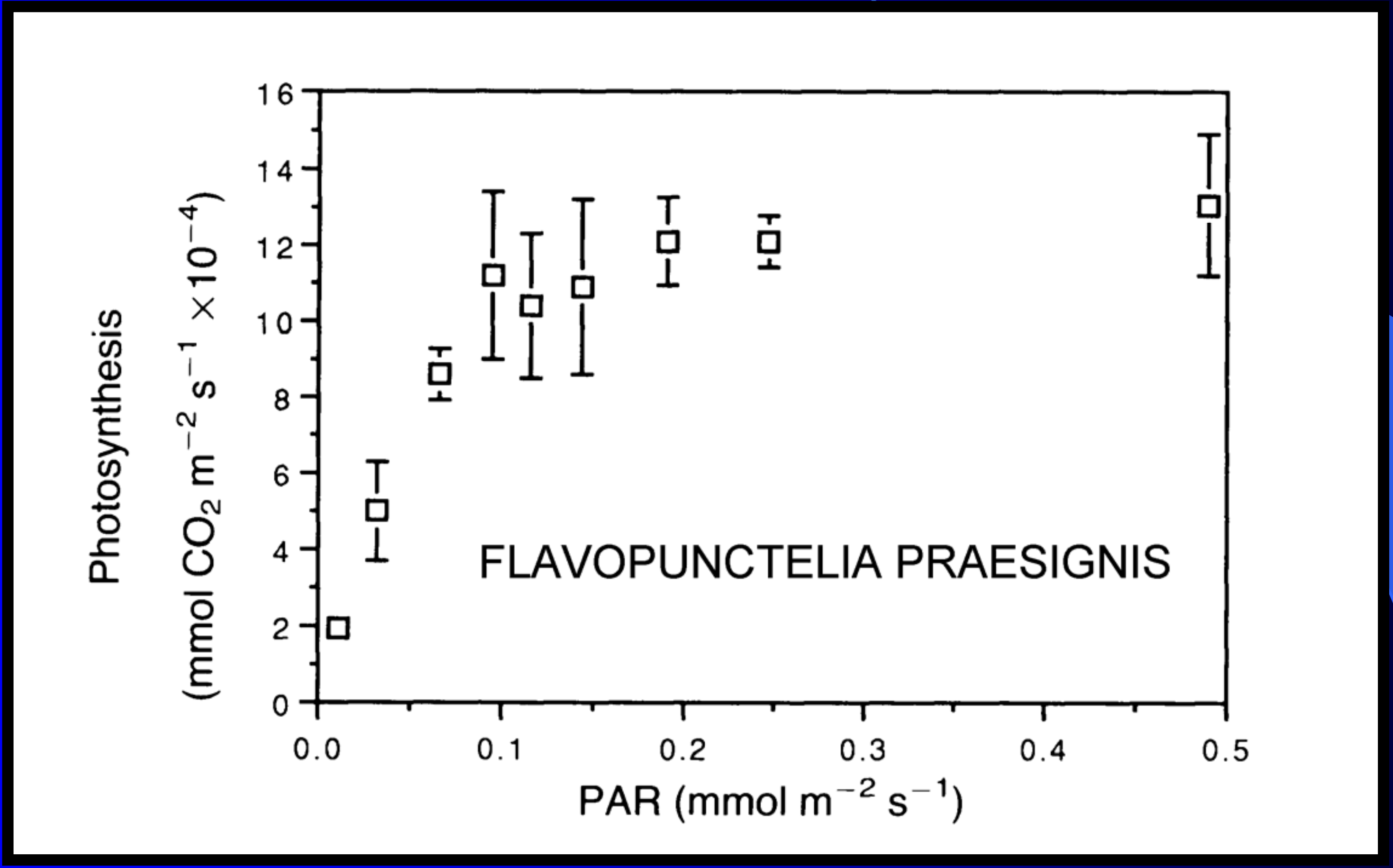



**Dependence of net photosynthesis in *Peltigera polydactyla* on thallus water content at four temperatures for three collections made across two months, beginning 1 March at Hamilton, Ontario.**

# Effects of Light on Rates of Gas Exchange

- Light is usually measured as PAR (**P**hotosynthetically **A**ctive **R**adiation)
- At a constant temperature, photosynthetic response to PAR exhibits a **saturation response**
  - Generally, lichens from sheltered habitats exhibit saturation at **lower** PAR than lichens in exposed niches.

# Dependence of net photosynthesis on PAR at 16ºC



# Effects of Light on Rates of Gas Exchange (cont.)

- Light saturation also varies with thallus water content:
  - 54-79% reduced penetration through the cortex when dry
  - 24-54% penetration when wet
  - This anatomical benefit may protect photobiont cells from injury due to high light intensities **and** the adverse effects of high temperature on $CO_2$ exchange mechanisms.

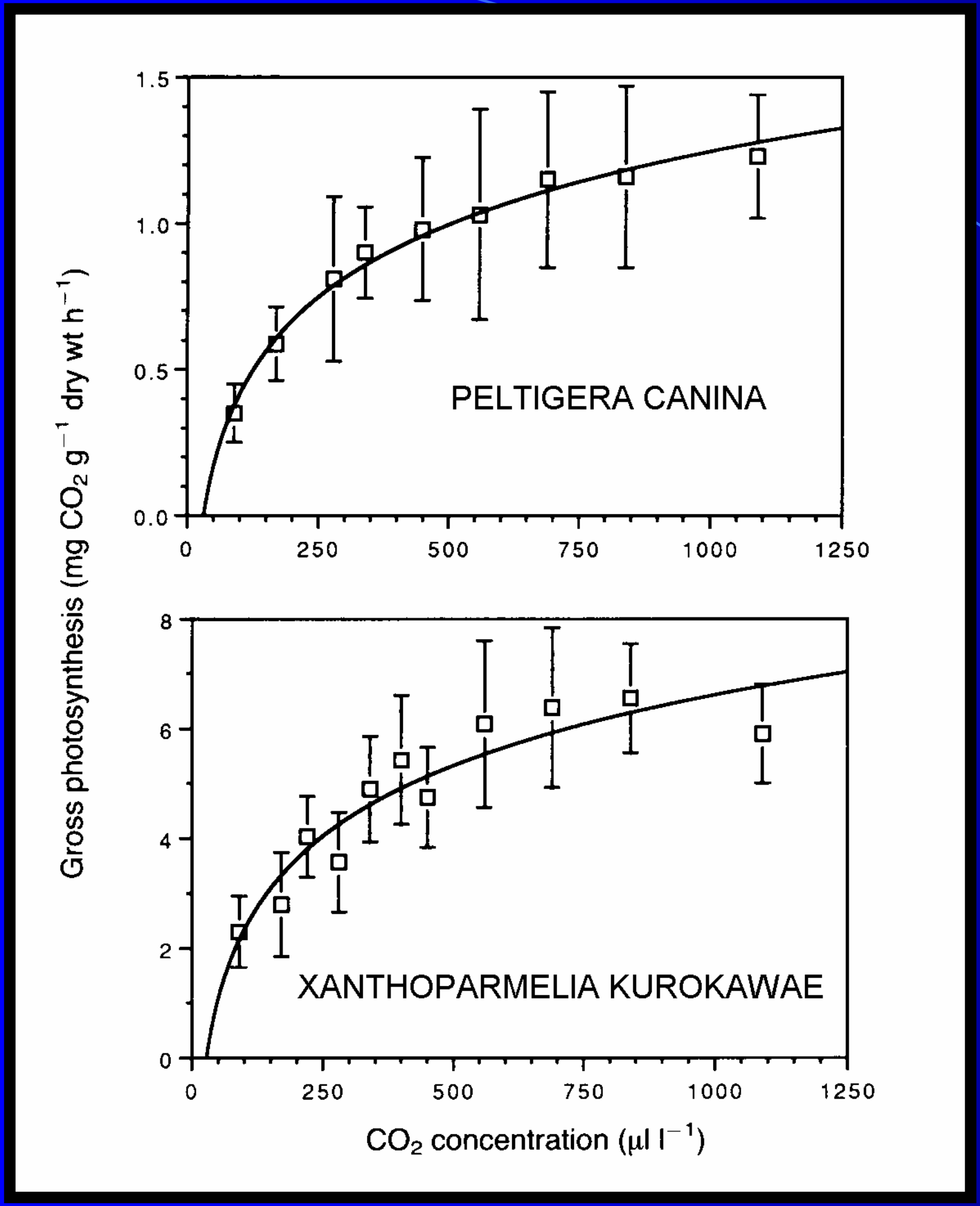
# Effects of Light on Rates of Gas Exchange (cont.)

- Lichens have been shown to "shift" the PAR saturation response to lower values with increasing shade (as in the forest canopy development in the spring).
- Lichens from shaded habitats vs. those from sunny areas exhibit many of the same responses as "sun" and "shade" leaves (thinner thalli, reduced pigmentation etc.)

# Effects of $CO_2$ Levels

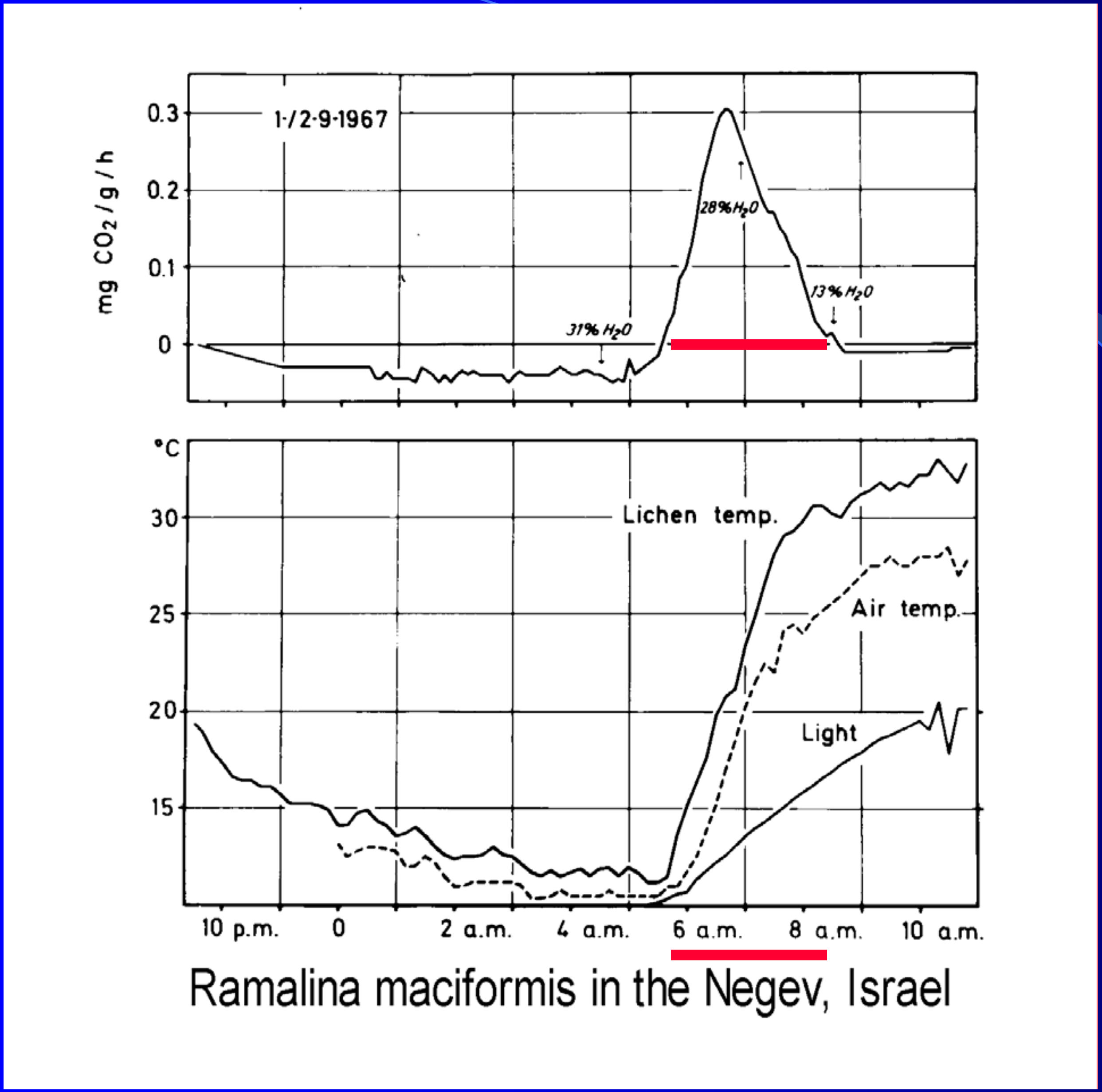
- Generally, there is an increase in photosynthesis with increasing $CO_2$ levels, at least up to 1200 ppm

# Dependence of gross photosynthesis on $CO_2$ concentrations



# $CO_2$ Effects (cont.)

- Rising $CO_2$ levels in lichen dominated ecosystems (as in the Arctic), may portend increased lichen growth and productivity.
- However, it is more important to calculate the time lichens will be in a favorable **moisture conditions** especially from fog and dew (something current prediction models fail to adequately address).




**Net carbon gain in most lichens occurs only for short periods.**

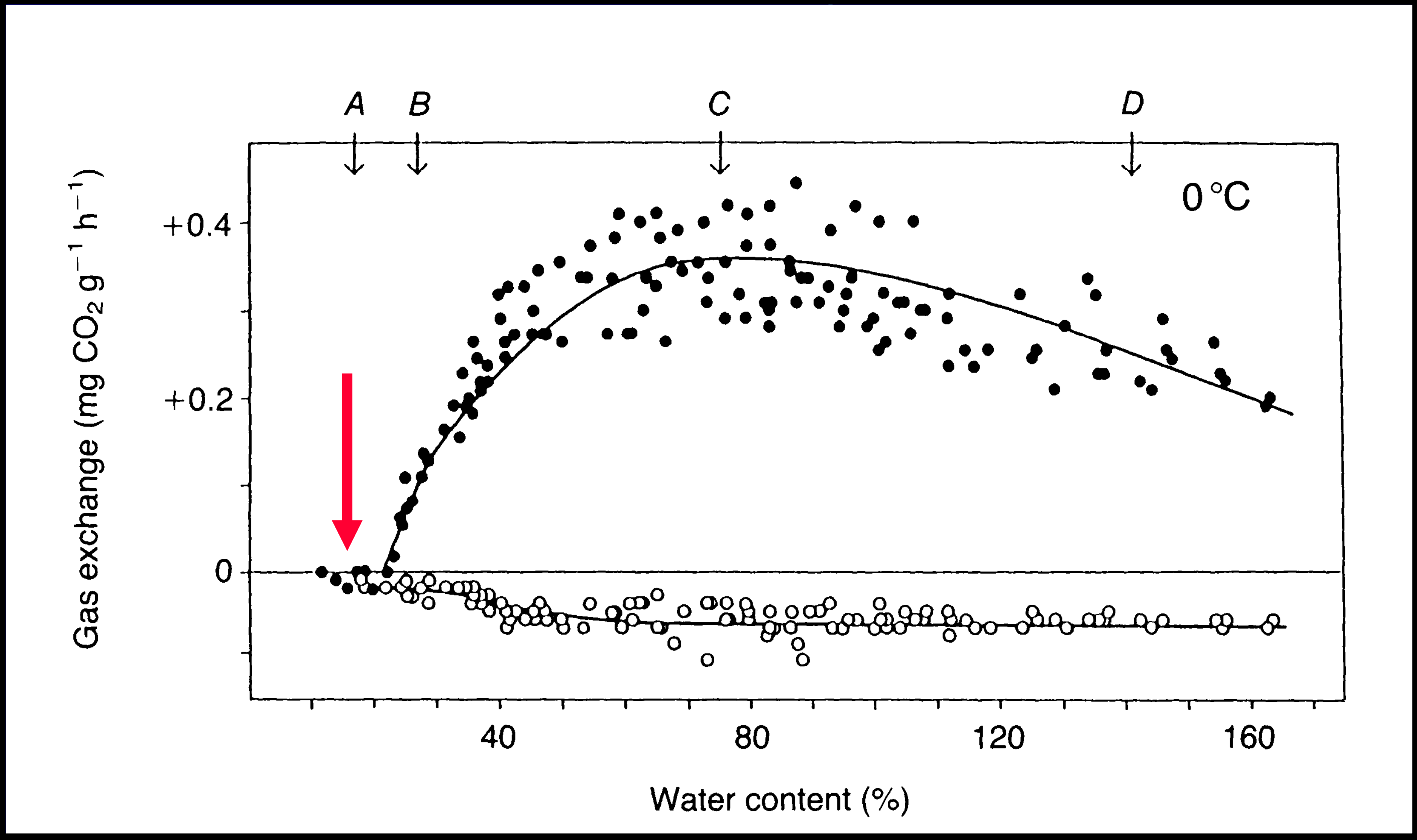
# DESICCATION

- Lichens (almost daily) alternate between **hydrated** and **desiccated** states
  - During the day, temperatures rise, humidity decreases
  - In the evening, humidity increases, temperatures decline
  - These changes take place gradually over hours

# DESICCATION (cont.)

- Early experiments showed a significant "**resaturation respiration**" response
  - When very dry thalli were immersed in water and $CO_2$ exchange measurements taken, the lichens showed several hours of $CO_2$ **release** before a net photosynthetic gain was established.
  - However, this is NOT the case under natural conditions and we discussed earlier.

# Natural Conditions



# Desiccation (cont.)

- Most lichens experience desiccation on a regular basis:
  - *Ramalina maciformis* in the Negev Desert can produce positive $CO_2$ uptake even with only early morning humidity and dew
  - Normally moist *Cladina* mats in the Arctic experience significant desiccation in the **UPPER portions** of the thallus (where most of the photosynthesis takes place)

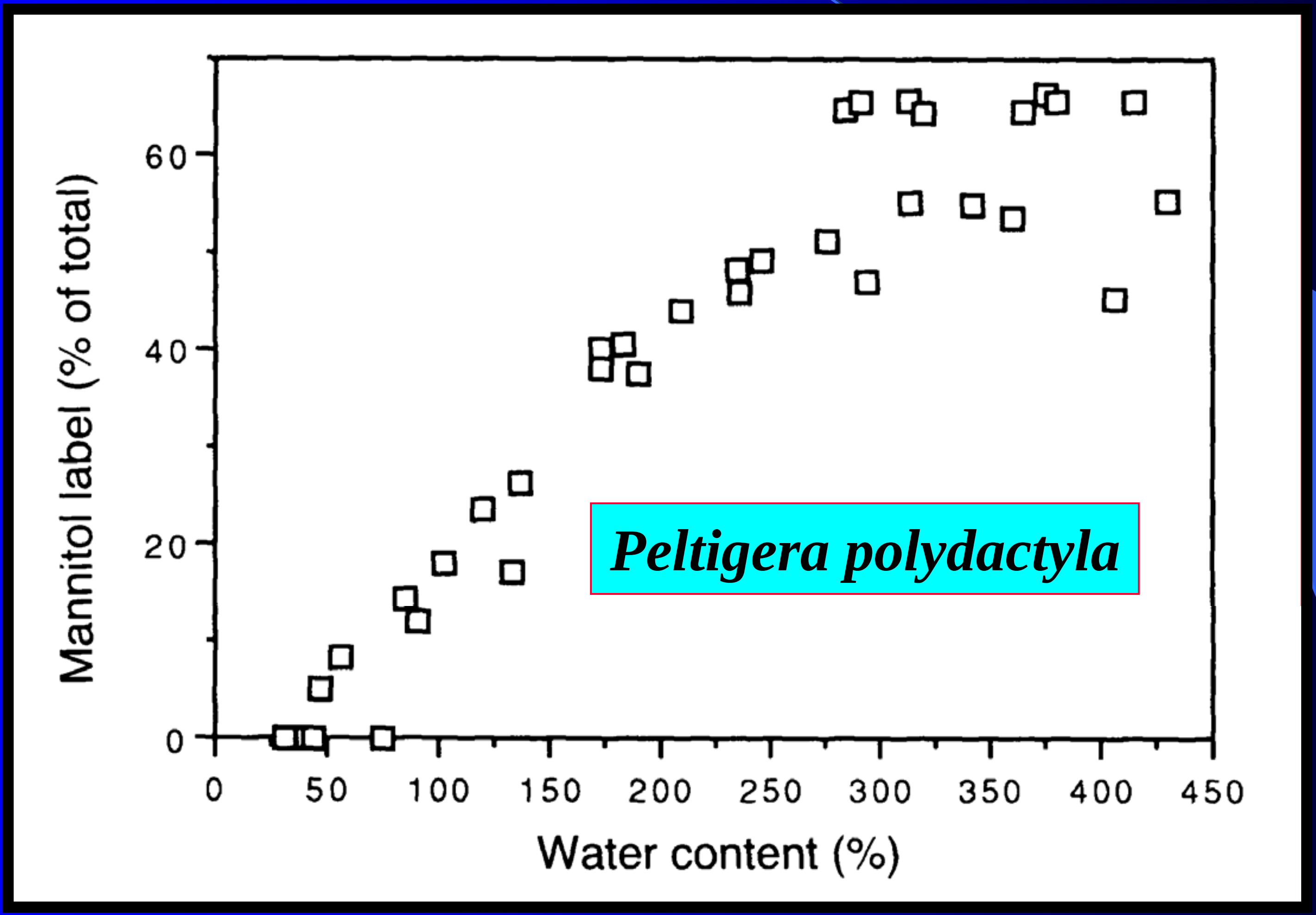
# Desiccation (cont.)

- Other examples:
  - *Ramalina maciformis* can survive storage for more than 1 year at 1% water content
  - Other taxa have survived more than 7 years in a desiccated state
- ***Why do lichens seem to do (grow) better with alternating hydration and desiccation?***
  - Many culture/greenhouse studies have confirmed this

# Desiccation (cont.)

- From studies on *Peltigera* species:
  - Greater **retention** of carbon within photobiont cells occurs at lower water contents
  - Greater **transfer** of carbon to the mycobiont occurs at intermediate to higher water content

# Amount of accumulated mannitol (manufactured in the mycobiont from photosynthetically produced glucose) in the thallus depends on thallus water content



# Desiccation (cont.)

- ***Therefore, alternating wet/dry cycles seems to ensure adequate distribution of fixed carbon between the two symbionts.***

# Desiccation (cont.)

- This requirement for wet/dry cycles is also supported by "submersion" experiments
  - *Hypogymnia physodes*, exposed to several days of submersion, showed a serious decline in photosynthesis, polyol content, and phosphorus uptake (no effect with wet/dry cycles)

# Desiccation (cont.)

El Niño rainfall events (as in the Galápagos Islands) have devastated many lichen populations.

# Desiccation (cont.)

- Desiccation effects can be created by **high solute concentrations**
  - Effects of “sea water” spray and “salty” atmospheric moisture can have significant desiccating effects on coastal populations
  - Different species have different tolerances for such conditions. *This may be partially responsible for controlling the ranges of certain taxa.*

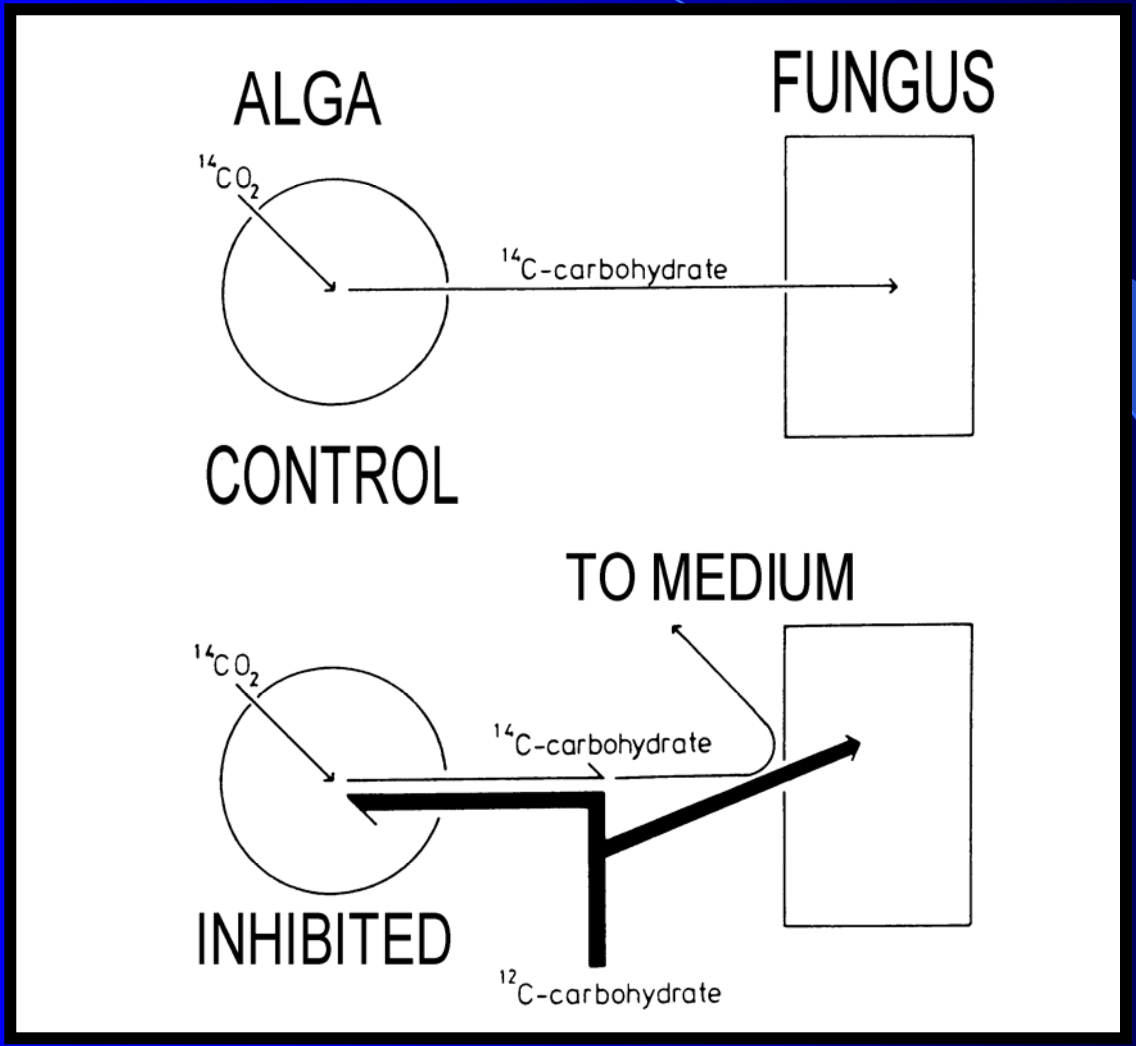
# CARBON TRANSFER

- Determination of which carbohydrates are transferred from the photobiont to mycobiont were first worked out using the "**inhibition technique**" by D. C. Smith
  - Lichen samples were placed in experimental dishes with $H^{14}CO_3^-$ ions
  - An alternative unlabeled carbohydrate was supplied to the lichen thallus samples in the growth medium

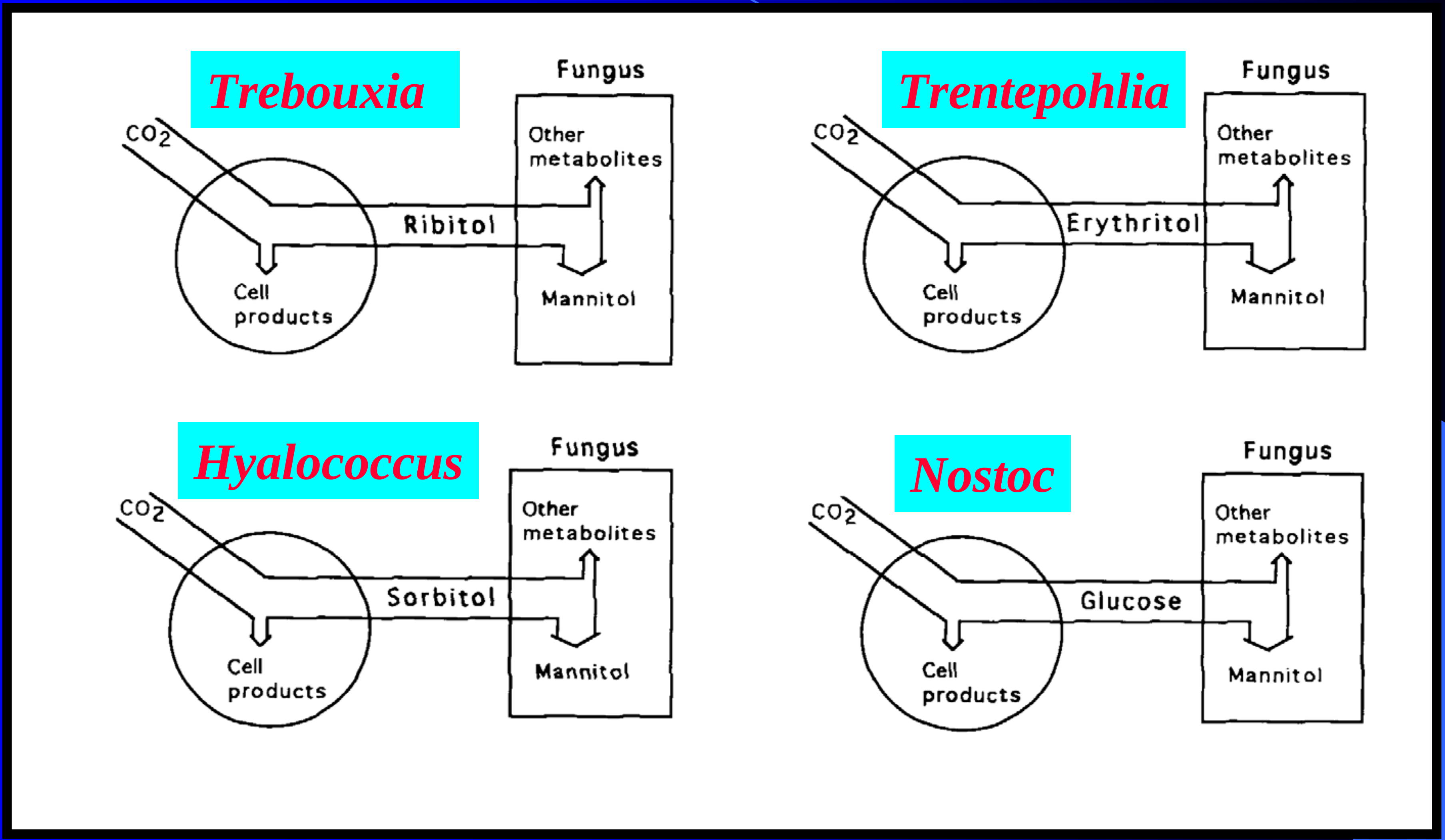
# CARBON TRANSFER (cont.)

- Uptake of fixed sugars from the photobiont using the $H^{14}CO_3^-$ ions accumulated in the medium rather than being taken up by the mycobiont
- The growth medium was analyzed for the presence of $^{14}C$ labeled carbohydrate compounds
- Different photobionts were shown to attempt to transfer different carbohydrates

# Inhibition Technique



# CARBON TRANSFER (cont.)



# CARBON TRANSFER (cont.)

- Initial measurements with high rates of transfer are misleading, since we now know that the rate is much slower in thalli with lower water contents.
- However, several experiments have shown that the fungus can stimulate the carbohydrate release (which slows considerably if the photobionts are isolated).
- The mechanism for this release phenomenon is still unknown.

# Productivity

- ***How much biomass do lichens actually contribute to ecosystems?***
  - **Examples:**
    - In old growth forests in the Pacific Northwest, *Lobaria oregana* was estimated at over 500 kg $ha^{-1}$ which translated to an estimate of 158 kg $ha^{-1}$ $yr^{-1}$
    - In lichen mats in the Arctic and Subarctic regions may reach 11,000-13,000 kg $ha^{-1}$
    - Of course, in some cases the value may be close to 0 (as in the cryptoendolithic lichens in the Antarctic)

# Lichen Growth and Growth Rates

- General approaches to this problem have been three-fold:
  - **Tracing studies**: using transparent materials, tracings of lichen thalli are done at intervals and annual growth rates calculated (usually as mm $yr^{-1}$ in foliose and crustose species; linear thallus increase in fruticose taxa)
  - **Photographic studies**: Photographs taken at intervals (with specific reference points) and compared with similar calculations made
  - **Use of dated substrates**: tombstones, monuments, etc.

# Lichen Growth and Growth Rates (cont.)

– Examples (general estimates):
  - FOLIOSE SPECIES: 0.5-4 mm $yr^{-1}$
  - FRUTICOSE SPECIES: 1.5-5 mm $yr^{-1}$
  - CRUSTOSE SPECIES: 0.5-2 mm $yr^{-1}$

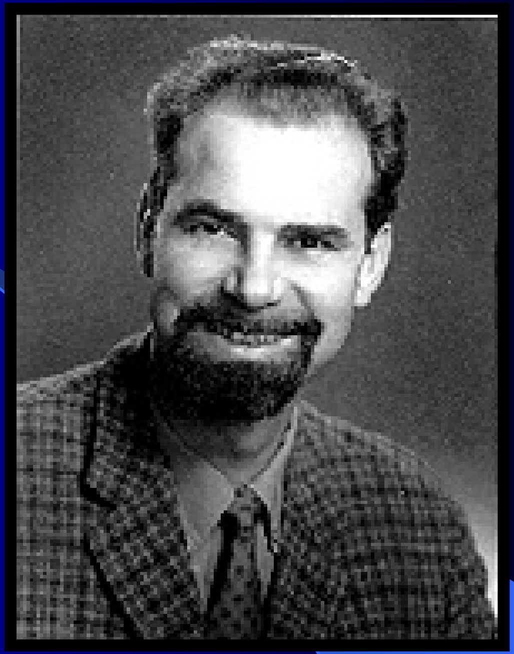
– Many taxa, however, will be much greater or much less depending on habitat
  - Some Arctic/alpine taxa which live more than 1,000 years have growth rates calculated in **mm per 100 years,** while some foliose and fruticose taxa have calculations ranging from **70-90 mm $yr^{-1}$**!

# Lichen Growth and Growth Rates (cont.)

- Although more data is needed, growth in most lichens follows a normal **sigmoid growth curve**, with an early slow juvenile stage, a middle linear growth phase and older plateau stage
- Lichen growth rates also shows **seasonal** and **annual** variation

# LICHENOMETRY

- Dating of substrates using lichen growth measurements
- *Rhizocarpon geographicum* group most widely used; also *Aspicilia* and *Lecidea* species



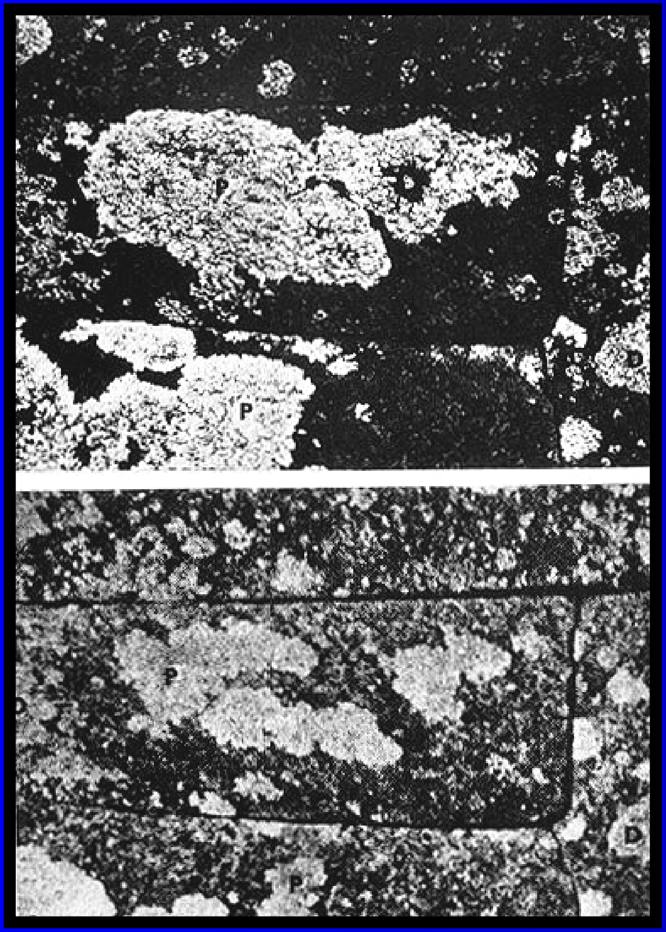
Roland Beschel, Queens University, Kingston, Ontario, pioneer worker in lichenometry (19??-1971)

# Lichenometry (cont.)

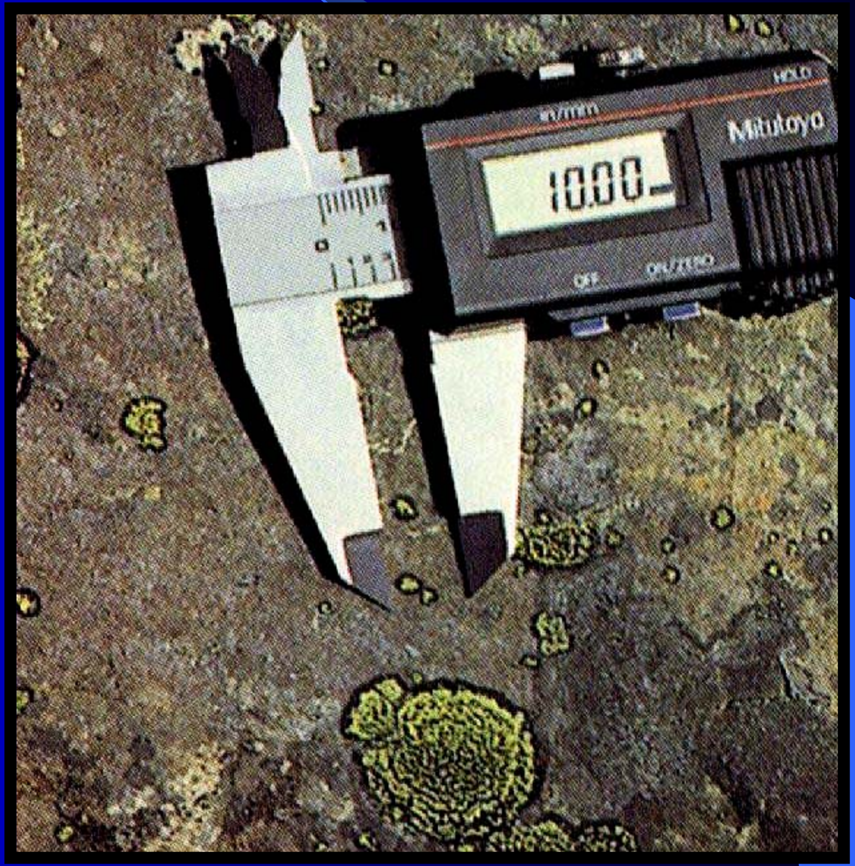
- Once a “growth curve” for an areas is established, many thallus measurements are made and plotted to determine age of the exposed substrate
- Technique used often by geomorphologists and archeologists

***Rhizocarpon***

# Lichenometry (cont.)



On Easter Island



# Lichenometry (cont.)

- Accuracy is sometimes questionable because of numerous unknowns, e.g.:
  - Initial date of colonization
  - Seasonal variation in growth rates
  - Growth rates changes with thallus age
- It has been used to date glacial movements, earthquakes, landslides, statues on Easter Island

# Lichenometry (cont.)

- Best results are obtained when growth curve data can be **correlated** with other dated structures (ancient graveyards, construction of European cathedrals etc.)
- Most active researcher in recent years has been J. L. Innes from Scotland.