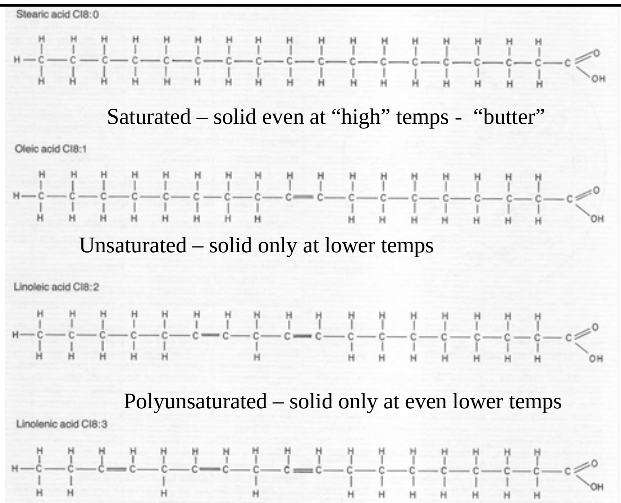


Saturated – solid even at “high” temps - “butter”

Unsaturated – solid only at lower temps

Polyunsaturated – solid only at even lower temps

4. The rate of dark respiration (which we have not yet talked about!) – CH2O + O2 -> CO2 + H2O – increases dramatically and non-linearly with temperature.

So Net photosynthesis, in addition to Gross Photosynthesis declines at high temperatures.

Temperature and photosynthesis: summary

1. Rubisco activity changes with temperature
2. O2 and CO2 solubility change with temperature, and so does photorespiration.
3. Membrane-associated function changes with temperature
4. Dark respiration changes with temperature

Outline for today:

Environmental impacts on Photosynthesis

1. From h20 to co2 limitations on photosynthesis
2. temperature
3. **Light**
4. nutrients

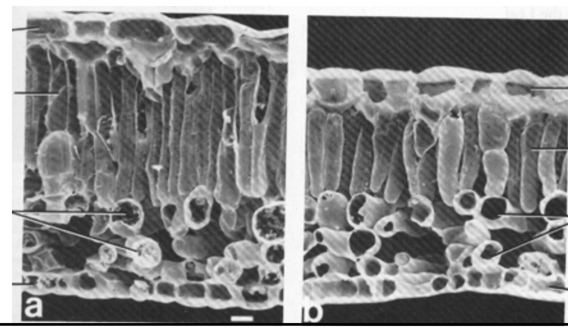
Light:

Note: This discussion of light influences on photosynthesis is restricted to photosynthetically-active radiation (400-700 nm).

Light has many other *indirect* impacts on photosynthesis, resulting from direct influences on leaf/canopy energy budgets, photo-period control of phenology, growth control by red/far red light ratios, etc. Those topics will be discussed later.

Light and Photosynthesis

1. The architecture and composition of leaves is related to short and long term light availability.



A cautionary note… light co-varies With other influences on leaf morphology

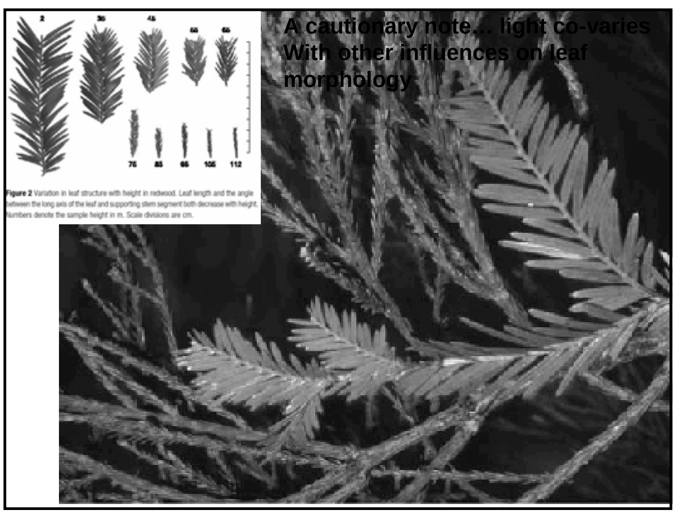
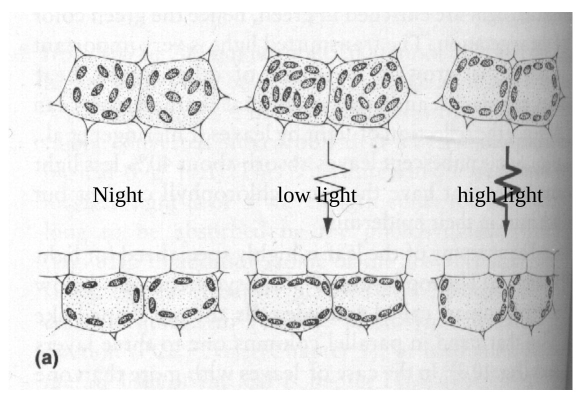


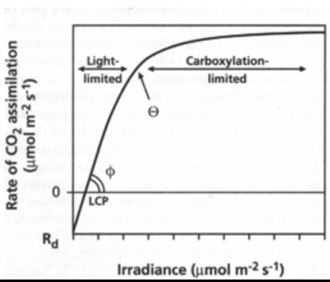
Figure 2 Variation in leaf structure with height in redwood. Leaf length and the angle between the long axis of the leaf and supporting stem segment both decrease with height. Numbers denote the sample height in m. Scale divisions are cm.

Light harvesting changes dynamically with light level



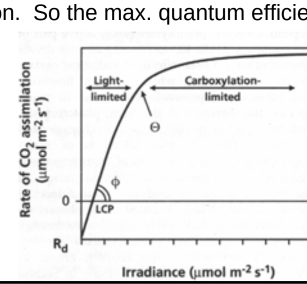
The light-response curve: dual-limitation analagous to CO2 limitations – light supply, and Calvin cycle limitation (any combination of CO2 supply and/or Rubisco/RuBP conc.

LCP = light compensation point – that light level needed to overcome the effects of photo and dark respiration.



The initial slope of the light response curve is called the apparent "quantum yield" in analogy to the yield we talked about earlier with isolated chlorplasts (.95).

Actual quantum yield for photosynthetic *products* is much lower, <0.1 CO2's for every photon. (This is a function of the fact that PSII needs 4 photons to split water, (2H2O -> O2 + 4H+ + 4e-), and PSI operates in step with PSII on each electron. So the max. quantum efficiency is 1/8 = .125)



The light response curve is useful because it allows us to quantify the functional difference between sun vs. shade leaves, or leaves adapted to different light environments, and to assess why sun/shade leaves function differently.

Let's take a look at some examples:

Acclimation vs. adaptation:

Note: quantum yield does not typically change – it is Amax that is altered.

Multiple ways to increase Amax.

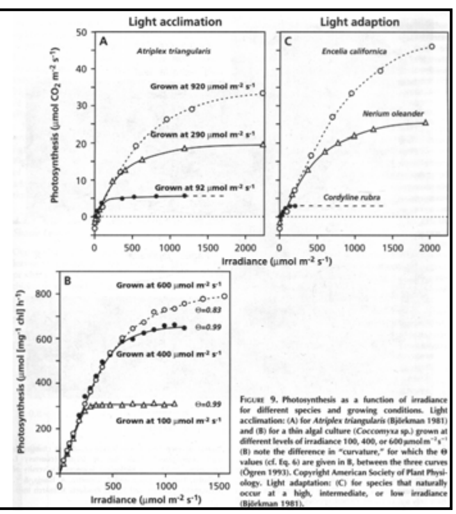


FIGURE 9. Photosynthesis as a function of irradiance for different species and growing conditions. Light acclimation: (A) for *Atriplex triangularis* (Björkman 1981) and (B) for a thin algal culture (*Coccomyxa* sp.) grown at different levels of irradiance 100, 400, or 600 μmol m^{-2} s^{-1} (B) note the difference in "curvature," for which the Θ values (cf. Eq. 6) are given in B, between the three curves (Ögren 1993). Copyright American Society of Plant Physiology. Light adaptation: (C) for species that naturally occur at a high, intermediate, or low irradiance (Björkman 1981).

Summary of differences in sun vs. shade leaves.

Overall pattern: sun leaves invest more in dark reaction components, shade leaves invest more in light harvesting components.

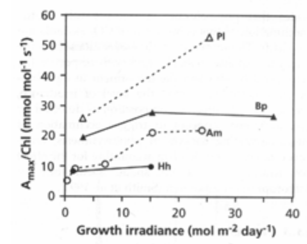
TABLE 2. Overview of generalized differences in characteristics between shade- and sun-acclimated leaves.

	Sun	Shade
Structural		
Leaf dry mass per area	high	low
Leaf thickness	thick	thin
Palisade parenchyma thickness	thick	thin
Spongy parenchyma thickness	similar	similar
Stomatal density	high	low
Chloroplast per area	many	few
Thylakoids per stroma volume	low	high
Thylakoids per granum	few	many
Biochemical		
Chlorophyll per chloroplast	low	high
Chlorophyll per area	similar	similar
Chlorophyll per dry mass	low	high
Chlorophyll a/b ratio	high	low
Light-harvesting Complex per area	low	high
Electron transport components per area	high	low
Coupling factor (ATPase) per area	high	low
Rubisco per area	high	low
Nitrogen per area	high	low
Xanthophylls per area	high	low
Gas exchange		
Photosynthetic capacity per area	high	low
Dark respiration per area	high	low
Photosynthetic capacity per dry mass	similar	similar
Dark respiration per dry mass	similar	similar
Carboxylation capacity per area	high	low
Electron transport capacity per area	high	low
Quantum yield	similar	similar
Curvature of light-response curve	gradual	acute

Light and photosynthesis: Ecological acclimation

The ratio Amax/Chl gives a rough indication of how much leaves invest in photosynthetic capacity to light harvesting capacity. 4 general behaviors are common:

1. Fast growing herbaceous species that survive subsequent shading: Amax/Chl starts high, decreases (PL)
2. Pioneer tree species always in the sun: maintain high A/Chl (BP)
3. Shade tolerant species that ultimately reach dominance (Am): increase A/Chl
4. Shade species: pretty inflexible: low A/Chl (Hh)



Nutrients and Photosynthesis

Nutrients and Photosynthesis

- Nitrogen is the nutrient plants need in the greatest amounts
- Most temperate ecosystems were N limited before humans came along.
- In leaf tissue, more than 50% of all Nitrogen is allocated in support of photosynthesis (proteins involved in light harvesting, electron transport and ATPase, Calvin cycle enzymes (including Rubisco).

•Indicates close r'ship between Photosynthesis and Nutrient Status

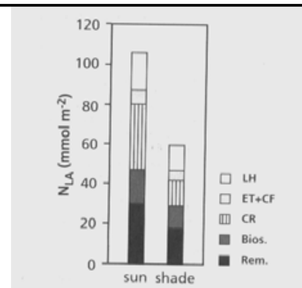
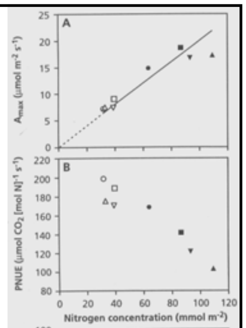


FIGURE 13. Nitrogen partitioning among various components in shade- and sun-acclimated leaves. Most of the leaf's nitrogen (here expressed per unit leaf area; NLA) in herbaceous plants is involved in the photosynthetic apparatus. Some of the fraction labeled Biosynthesis and Remainder is indirectly involved in synthesis and maintenance processes associated with the photosynthetic apparatus. LH = light harvesting (LHC, PSI, PSII), ET + CF = electron transport components and coupling factor (ATPase), CR = enzymes associated with carbon reduction (Calvin cycle, mainly Rubisco), Bios = Biosynthesis (nucleic acids and ribosomes), Rem = remainder, other proteins and nitrogen-containing compounds (mitochondrial enzymes, amino acids, cell-wall proteins, alkaloids, etc.)

Nutrients and Photosynthesis

- Photosynthetic capacity is strongly correlated with leaf Nitrogen concentration. (Figure A).
- N starved leaves have high Photosynthetic Nitrogen Use Efficiency – N rich leaves are 'wasteful'
- How exactly does N control A?



Not by a simple, direct mechanism. More of a integrated leaf response.

When leaf N is varied, A-ci curves generally continue to show co-limitation to Photosynthesis by Carboxylation and RuBP regeneration.

This indicates a coordinated down-regulation of the entire photosynthetic process.

Nitrogen content correlates strongly with leaf life span, reflecting the cost of investment in N.

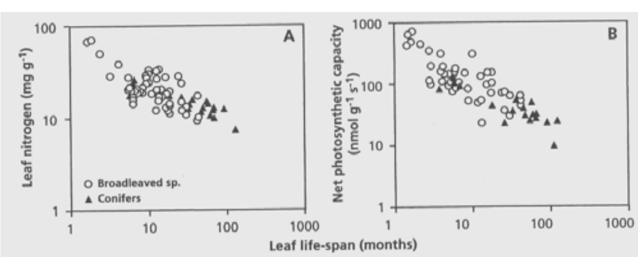


FIGURE 33. Mass-based leaf nitrogen (A) and maximum rate of CO_2 assimilation (B) as a function of leaf lifespan in broadleafed and confier trees (Reich et al. 1995). Copyright Academic Press.

Dark Respiration

Primarily, function of respiration is:
$CH_2O + O_2 \rightarrow CO_2 + H_2O$ + energy

(Energy embodied in ATP)

Dark Respiration represents a substantial portion of a plant's carbon budget.

TABLE 1. Utilization of photosynthates in plants, as dependent on the nutrient supply.

Item	Utilization of photosynthates % of C fixed	
	Free nutrient availability	Limiting nutrient supply
Shoot growth	40*–57	15–27*
Root growth	17–18*	33*–35
Shoot respiration	17–24*	19–20*
Root respiration	8–19*	38*–52
• growth	3.5–4.6*	6*–9
• maintenance	0.6–2.6*	?
• ion acquisition	4–13*	?
Volatile losses	0–8	0–8
Exudation	<5	<23
N_2-fixation	negligible	5–24
Mycorrhiza	negligible	7–20

Source: Van der Werf et al. 1994.
*, inherently slow-growing species; ?, no information for nutrient-limited conditions.

Dark Respiration

-Biochemistry of respiration

Glycolysis ("glyco"=sugar; "lysis"= "untie")

Citric acid cycle ("Krebs cycle")

Electron transport and ATP synthesis

-Respiration and carbon economy of whole plants

Hans Krebs, 1953 Nobel Prize

Significance of Krebs' contribution (from nobelprize.org)

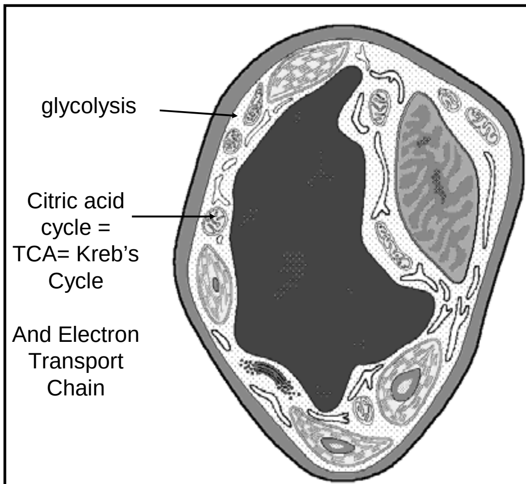
- Prior to the speech, G. Liljestrand, Member of the Royal Academy of Sciences, addressed the laureate:

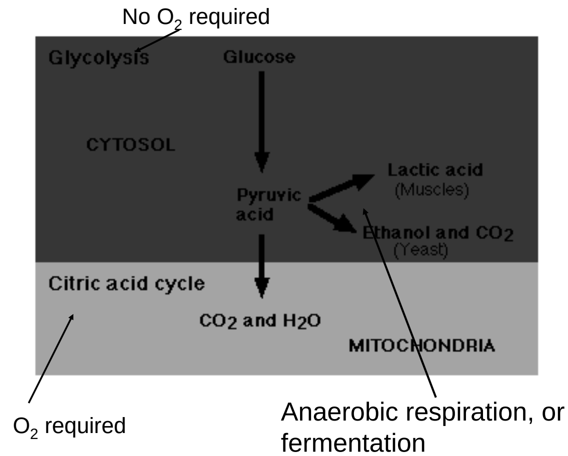
"Few processes are more fundamental than the slow burning or oxidation of organic matter in our body. And yet the intimate mechanism of this stepwise disintegration is only very incompletely known. Thanks to the investigations of Professor Krebs and Professor Lipmann, new light has been shed on what is actually going on. We have learnt that suitable fragments of our foodstuffs become incorporated in the so-called Krebs cycle where they will be able to act as the fuel of life. And Professor Lipmann has taught us the prominent role in this connection of one of those mysterious substances which occupy a key position in the living organism. His coenzyme A is a necessary link in the transformations of some substances into the Krebs cycle as well as in many other processes. These are fundamental discoveries, but the layman will probably ask for some immediate practical application. We may answer with the counterquestion of Benjamin Franklin: "What is the use of a new-born baby?"

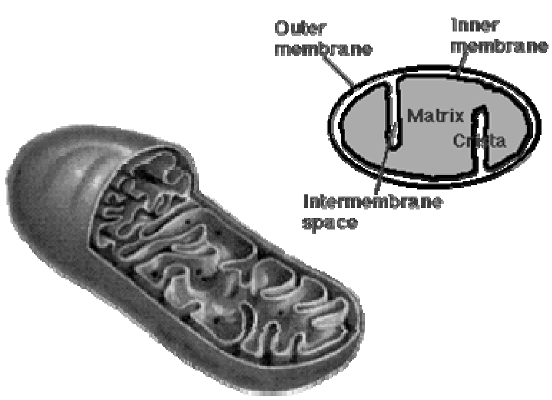
Glycolysis – break a 6-carbon sugar into two 3-Carbon sugars (triose phosphate) – takes some energy – then strip electrons from these 3-C sugars – releases a bit of energy in the form of ATP and NADH. "Leftover" products: 3C sugars Pyruvate and Malate (still embody substantial free energy)

Citric acid/krebs cycle complete *oxidation* of pyruvate/malate to produce CO2, H2O, reducing power (NADH, FADH2) and ATP

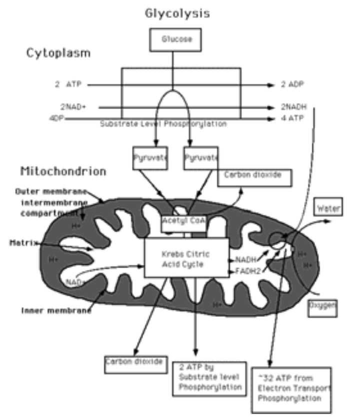
Electron Transport Chain launder NADH, FADH2 to ATP across inner mitochondrial membrane



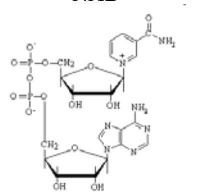




There is evidence that glycolysis predates the existence of O_2 in the Earth's atmosphere and organelles in cells (it happens in the cytoplasm, not in some specialized organelle) and it is a metabolic pathway found in all living organisms.



NAD+

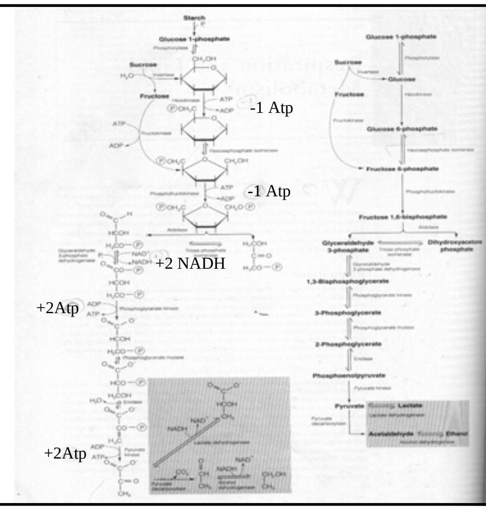


Step 1:
ATP, NADH production in Glycolysis:

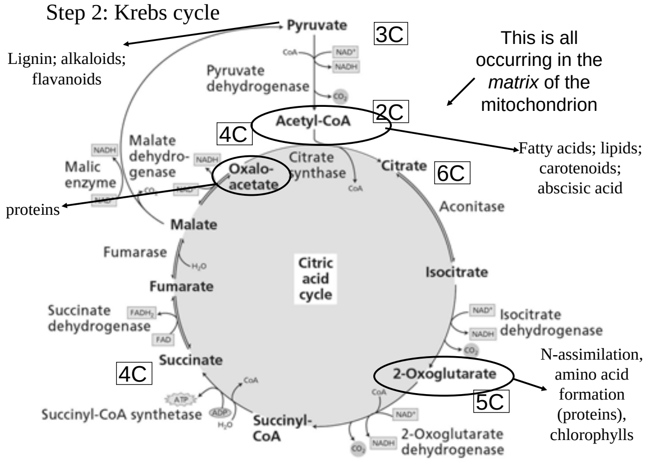
Takes some to get some…and not very much

Net: 2 ATPs, 2 NADH's per glucose or fructose.

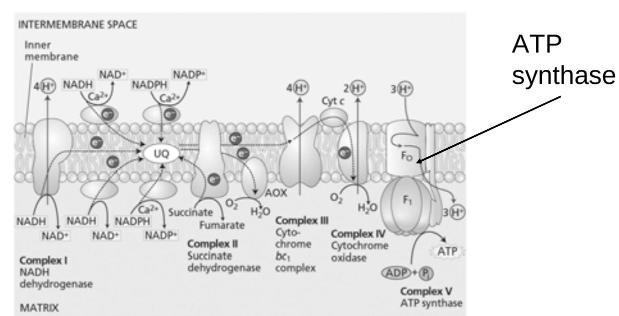
Net:
-1ATP-1ATP+2ATP+2ATP = 2ATP



Step 2: Krebs cycle



Step 3: Electron transport chain

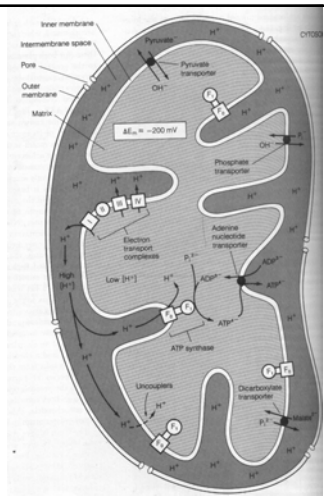


Most of the ATP produced in respiration comes from electrons of NADH and FADH2 that enter a membrane-bound electron transport process, producing a membrane potential, leading to oxidative phosphorylation

Where this is all happening:

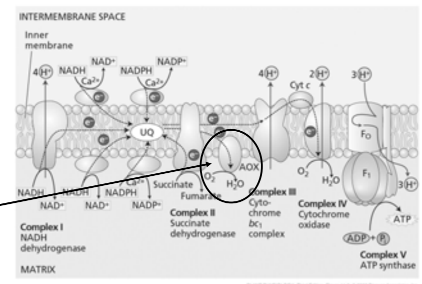
Glycolysis: cytosol
Krebs: matrix (inside inner membrane)
Electron transport: across inner membrane.

ATP generation: same process as in photosynthesis (“oxidative phosphorylation”, aka Mitchell’s chemiosmotic pump)



An “alternate path” (aka, the cyanide resistant path) de-couples respiratory electron transport from ATP production. This pathway consumes O_2, but doesn’t produce ATP. It can serve as an “energy overflow valve” when supply exceeds demand – but it results in a net loss of energy from the plant. Is this a relic “error” or an important physiological function?

An “alternative oxidase” (AOX) accepts electrons coming from complex II, preventing them from getting to complex III



Comparing energy yield:

1 mol glucose gives
ΔG^o = -2880 kJ/mol
1 mol ATP takes
ΔG^o = 50.2 kJ/mol

Glycolysis (per glucose):
Net: 2ATP, 2NADH

Krebs (per glucose):
2ATP, 8NADH, 2FADH2

Total: 4ATP, 10NADH equivalents
ATP:NADH ratio ~3 in Mitochondria. Thus 4ATP + 10NADHx3 = 34 ATPs per glucose (more or less)

34 x 50.2 kJ/mol / 2880 kJ/mol = 59% conversion efficiency! (versus around 4% for glycolysis alone)

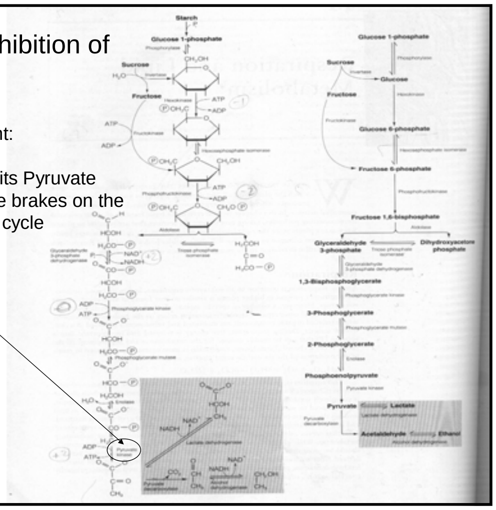
Feedback control of Respiration:

Demand regulation: low amounts of ADP dramatically reduce the rate of mitochondrial respiration (when energy demand for growth, maintenance and transport processes is high, ATP is rapidly consumed, producing ADP, which increases the rate of respiration)

Feedback inhibition of respiration

A key control point:

Large [ATP] inhibits Pyruvate kinase, putting the brakes on the fuel for the Krebs cycle



Mitochondrial electron transport is controlled by both “supply” (availability of carbohydrates and organic acids) and “demand”– (energy requirements for growth, maintenance and transport processes)

Respiration and Plant Carbon Balance

On a whole-plant basis, respiration consumes from 30% to 70% of total fixed carbon

Leaves account for about half of the total

(Is it possible to increase net growth by reducing respiration rates?)

Environmental Factors Influencing Respiration

•Anoxia
•Temperature
•CO2
•Nutrient Stress
•Salt

The amount of photosynthate consumed in respiration varies with tissue type and with environmental conditions.

When nutrients are limiting, respiration rates in roots increase dramatically.

	Utilization of photosynthates % of C fixed	
Item	Free nutrient availability	Limiting nutrient supply
Shoot growth	40*–57	15–27*
Root growth	17–18*	33*–35
Shoot respiration	17–24*	19–20*
Root respiration	8–19*	38*–52
• growth	3.5–4.6*	6*–9
• maintenance	0.6–2.6*	?
• ion acquisition	4–13*	?
Volatile losses	0–8	0–8
Exudation	<5	<23
N_2-fixation	negligible	5–24
Mycorrhiza	negligible	7–20

Source: Van der Werf et al. 1994.
*, inherently slow-growing species; ?, no information for nutrient-limited conditions.

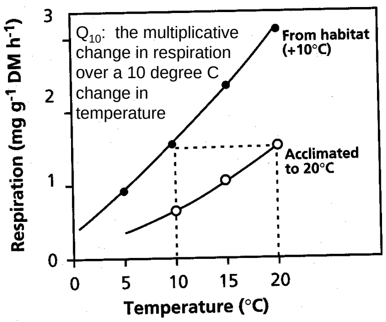


FIGURE 17. Temperature response of respiration of *Vaccinium myrtillus* (bilberry) shoots of populations acclimated to 10°C and 20°C. The dashed line shows the respiration rate of each plant at its acclimation temperature (Körner & Larcher 1988). Copyright The Company of Biologists.

Mitochondrial Respiration (like photorespiration) increases rapidly with temperature. Can this lead to reduced growth at high temperatures?

Maybe, but most likely only in extreme cases. Respiration "generally" acclimates to changes in temperature.

LCP p. 119

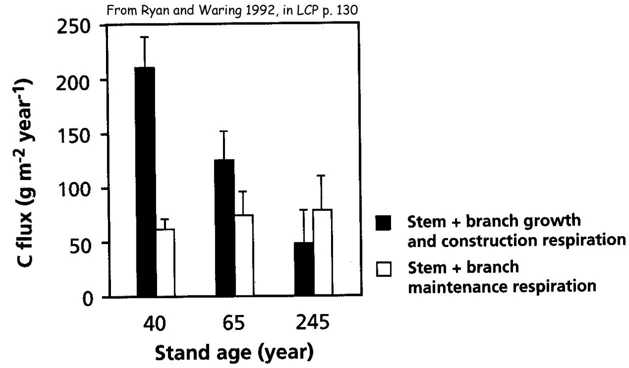
Respiration is often subdivided into Growth, Maintenance and Transport costs

Growth respiration: (a.k.a. "construction respiration") – a "fixed cost" that depends on the tissues or biochemicals that are synthesized. Often described in terms of "glucose equivalents"

Maintenance respiration: The cost of maintaining existing tissues and functions, (Protein turnover is the largest cost of maintenance respiration)

Do high maintenance "costs" reduce growth of large trees?

From Ryan and Waring 1992, in LCP p. 130



Evidence appears unlikely, even though most textbooks cite respiration as the cause of growth decline in trees/forests