Carbon Cycle, part 2
Ecophysiology of Leaves

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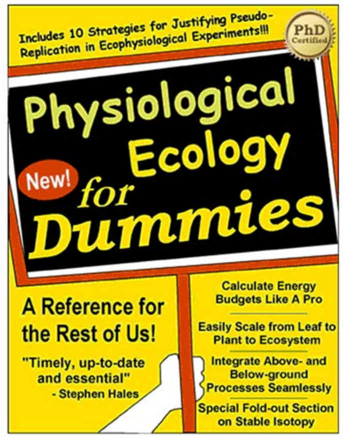


Courtesy of Rob Jackson, Duke

Outline

- Photosynthetic Pathways and Cycles
- Environmental Physiology of Photosynthesis
  - Light
  - Temperature
  - CO_2
  - Nutrients
  - Soil Moisture and Water Deficits
- Respiration

Basic Photosynthesis Stoichiometry

$$6CO_2 + 6H_2O + (light) \rightarrow (C_6H_{12}O_6) + 6O_2$$

Basic stoichiometric equation on photosynthesis and the production of sugar and oxygen via the consumption of CO2, water, and light

Physiological Attributes of Plants

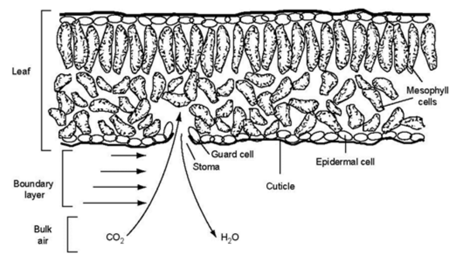
- **photosynthetic pathway**
  - C_3
  - C_4
  - CAM






Several pathways exist for fixing CO2 into sugar

Photosynthesis:
A balance between Supply and Demand



- Biochemical limitation: carboxylation rate
  - Light limitation
  - Enzyme limitation
- Physical limitation: delivery of CO_2 to leaf
  - Diffusion through Leaf Boundary Layer
  - Diffusion through Stomatal Pores
  - Potential Gradient between free Atmosphere and substomatal Cavity

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Photosynthesis is more than just the simple equation and the presence of light. There is a balance between the rates of photosynthesis due to the supply of CO2 in the air, its diffusion through the mesophyll, stomata and leaf surface boundary layers and the demand for CO2 by light and the photosynthetic capacity of the leaf, due to its thickness, amount of N in Rubisco and layers of mesophyll cells with chlorophlasts.

Critical Steps in C_3 Photosynthesis
Calvin-Benson Cycle

- Light Reactions
  - Chlorophyll, in chloroplasts, captures photons
  - Light energy is used to produce chemical energy in the forms of NADPH and ATP
  - Oxygen is produced
- Dark Reactions
  - A 3-C compound, PGA, is formed at the first Carboxylation step via the reaction between CO_2 and RUBP, a C_5 compound, and its subsequent cleaving (C_6 => 2 C_3)
  - The enzyme RUBISCO catalyzes the reaction between CO_2 and RUBP
  - RUBISCO has an affinity for both CO_2 and O_2, with the later leading to photorespiration, a loss of CO_2
  - RUBISCO accounts for about 9 to 25% of the N in a leaf
  - Chemical Energy (NADPH & ATP) is used to regenerate RUBP

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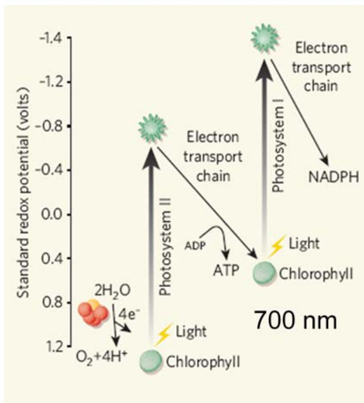
The enzyme ribulose-1,5-bisphosphate carboxylase (rubisco) catalyzes the addition of gaseous carbon dioxide to ribulose-1,5-bisphosphate (RuBP). Product of the reaction are two molecules of 3-phosphoglyceric acid.

$C_5O_3H_8(PO_4^{2-})_2 + CO_2 \text{ -> } 2\ C_3O_3H_4PO_4^{2-}$

Using Solar Energy for Life

Light ('Hill') Z Reactions:
PS II and Ps I

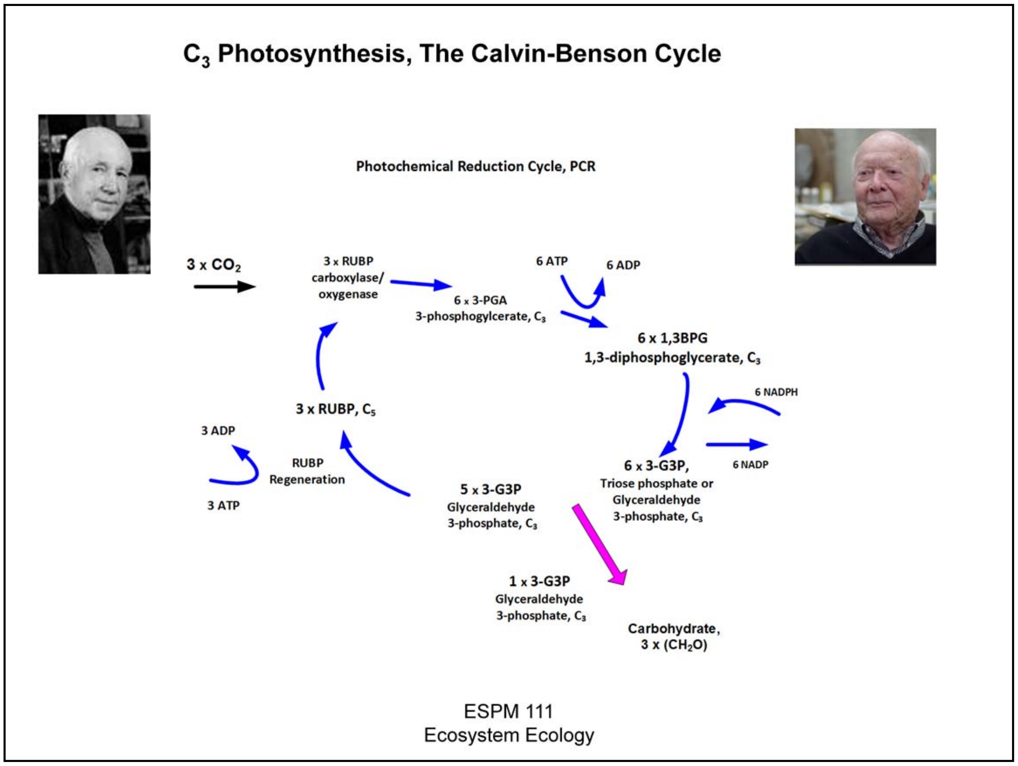


680 nm

- Visible solar energy (400 to 700 nm) is absorbed by pigments
- This energy is converted into high energy compounds, ATP and NADPH, by photosystems II and I (PS II and I)
  - Photosystem II uses 680 nm energy to generate ATP (non-cyclic electron transport)
  - PS I uses 700 nm solar energy to generate NADPH (cyclic electron transport).
  - Excess energy is lost as heat or fluorescence.
- 8 Photons per CO_2 molecule fixed

Allen and Martin, 2007 Nature

Basics of the light reactions



An example of the stoichiometry of the photosynthetic carbon reduction (PCR) and the photosynthetic carbon oxidation (photorespiration cycles). In this case, it is scaled with in an input of 3 CO2 molecules

The enzyme ribulose-1,5-bisphosphate carboxylase (Rubisco) catalyzes the reaction between gaseous carbon dioxide and ribulose-1,5-bisphosphate (RuBP).

Product of the reaction are two molecules of 3-phosphoglyceric acid for each CO2 molecule

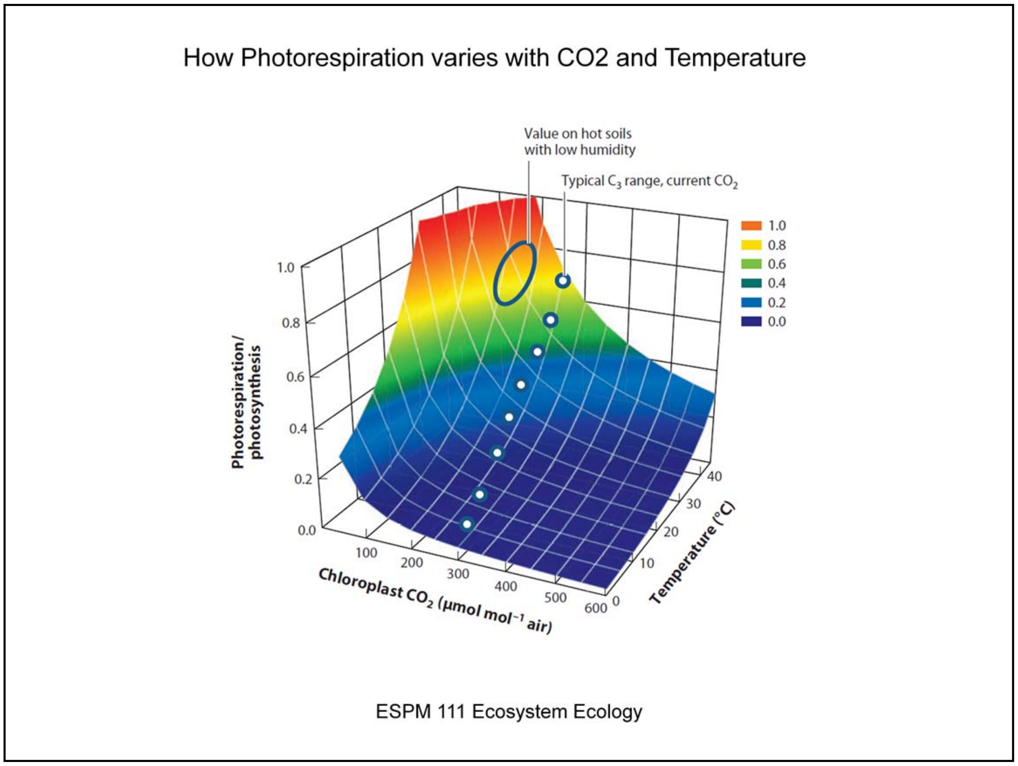
$C_5O_3H_8(PO_4^{2-})_2 + CO_2 \rightarrow 2\ C_3O_3H_4PO_4^{2-}$

RUBISCO has an affinity for both CO_2 and O_2, with the later leading to photorespiration, a loss of $CO_{2.}$ The rate of competitive oxygen fixation is a proportional to the oxygen concentration time the ratio of oxygenation (Vo) to carboxylation (Vc). At ambient conditions Vo/Vc is about 0.27 (2 times the CO2 compensation point divided by CO2; ~ 2 x

38/280). In practice for each CO_2 consumed by carboxylation 0.5 CO_2 times Vo/Vc are lost by photorespiration; hence the amount of photorespiration decreases as CO_2 concentrations increase

Chemical Energy (NADPH & ATP) is used to regenerate RUBP

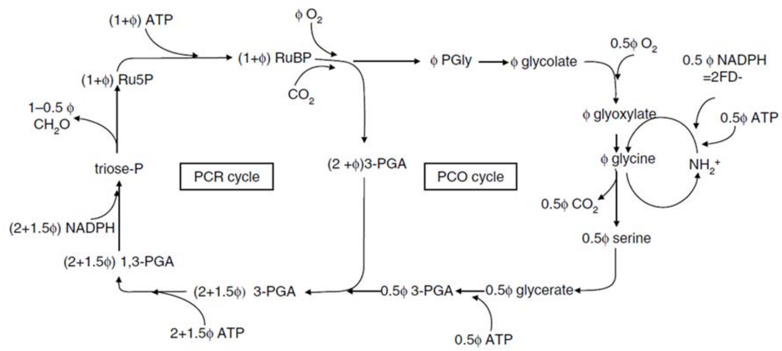
Resource: von Caemmerer. 2000. Biochemical models of leaf photosynthesis, CSIRO Publishing



Graphic showing how photorespiration Increases with higher Temperature and lower CO2.

Sage et al 2013

Photosynthetic Reduction/Oxidation Cycles

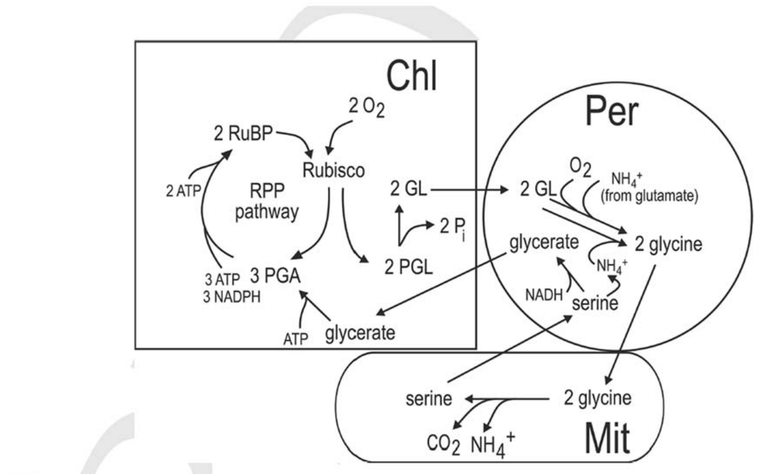


Von Caemmerer, Farquhar and Berry, 2009, In: Photosynthesis in silico

ESPM 2, The Biosphere

Pathway linking photosynthetic carbon reduction and photosynthetic carbon oxidation cycles

PhotoRespiration



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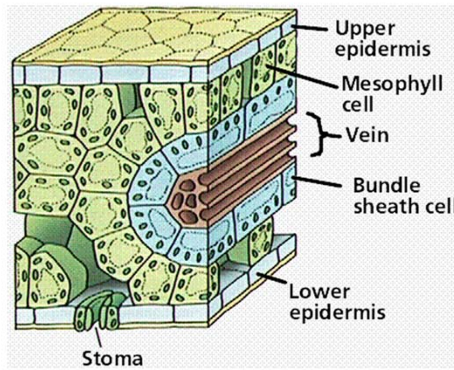
More gory biochemical detail on photorespiration for those interested

C_4 leaf



http://www.emc.maricopa.edu/faculty/farabee/BIOBK/C4leaf.gif

C4 photosynthesis evolved with a change in leaf anatomy too, the bundle sheaths of the kranz anatomy.

Facts about C4 Plants

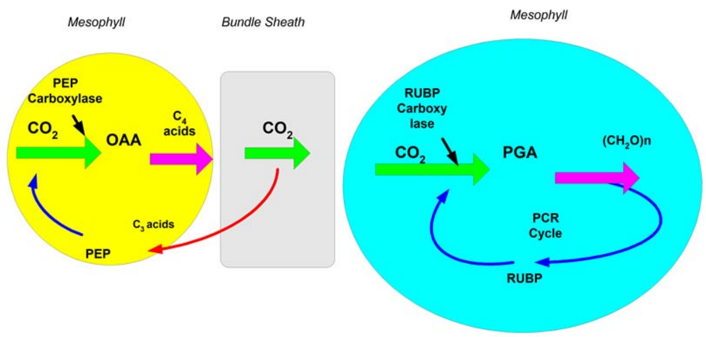
- C4 photosynthesis has had 66 independent origins
- Accounts for 23% of global GPP
- Is associated with 7500 species out of 250,000 plant species
- Evolutionary origin: C4 dominated ecosystems existed about 10 Million years ago;
- Species present up to about 33 Million years ago

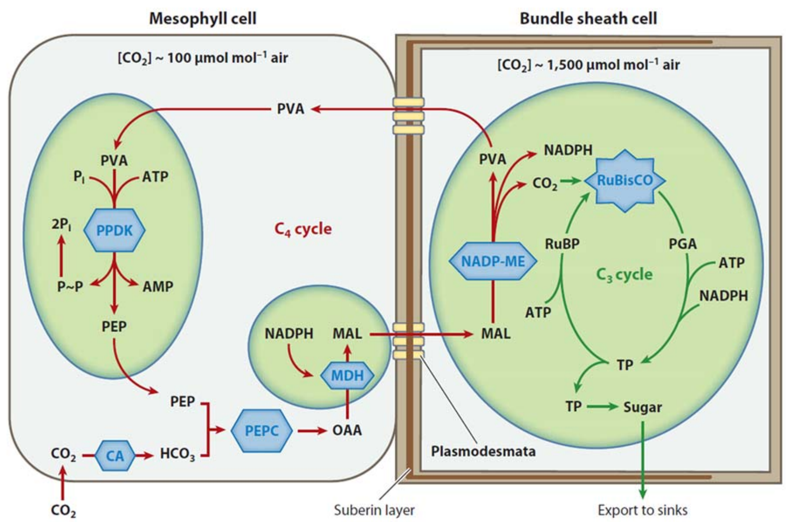
Sage et al 2013 Ann Rev Plant Biology on C4..

Critical Steps in C_4 Photosynthesis

- The enzyme PEP Carboxylase catalyzes a reaction between CO_2 and phosophenolpyruvate (PEP) to form a C_4 compound
- The C_4 compound is transported into the specializes cells, the bundle sheaths, and is decarboxylated
- CO_2 is released into an environment and photosynthesis is completed via the C_3 cycle
- Photorespiration is low; RUBISCO favors CO_2 in this environment because the ratio between CO_2:O_2 is high

C_4 Photosynthesis





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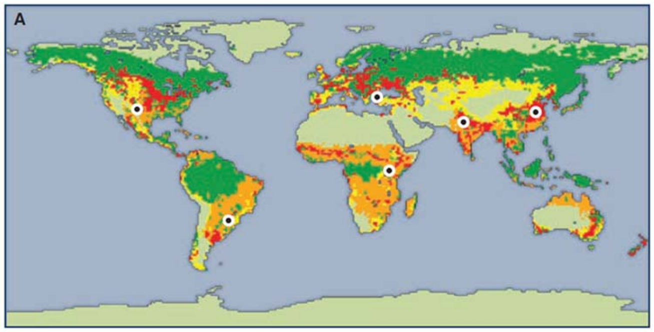
After Sage et al 2013 Annual Review Plant Biology

C3 vs C4 Grass Distribution



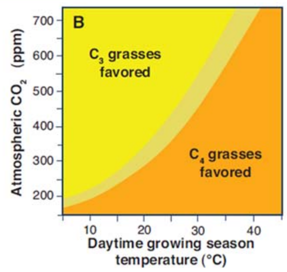
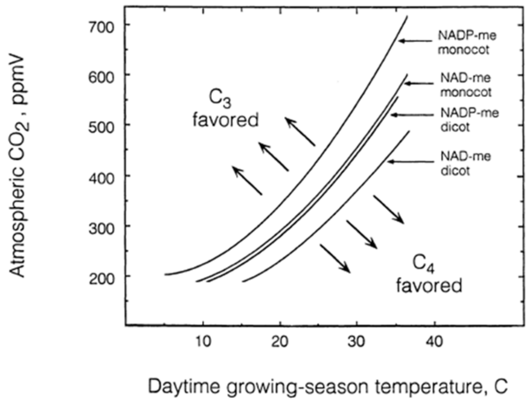


Fig. 1. (**A**) Global distribution of forests (green) and woodlands, savannas, and grasslands with a ground cover dominated by either C_4 (orange) or C_3 (yellow) grasses. Cropland (red) and shrubs, desert, bare ground, and ice (beige/brown) are also shown. See the supporting online material (SOM) (*49*) for a full description of land-cover data and its categorization. White circles with black dots in the center indicate the regions in which the geological history of C_4 grasslands is best described (see Fig. 3). (**B**) The predicted atmospheric CO_2 and growing-season temperature conditions that favor the growth of C_3 or C_4 grasses, based on the quantum yield of photosynthesis, a measure of the inefficiency caused by photorespiration [adapted from (*10*)].

Edwards et al 2010 Science

Why are CA Hot Grasslands Compose of C3 grasses?



CA annual Grasslands experience cool wet winter growing season

Adapted from Ehleringer et al. 1997

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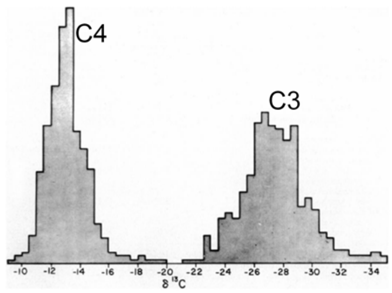
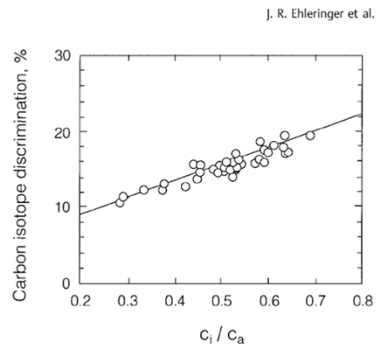
Question. Are C4 grasses favored in California?

C3 vs C4: Isotopes and Ci/Ca



O'Leary, 1988 Bioscience



Tool to Study Advance and Retreat of C3 Grasslands During Ice Age

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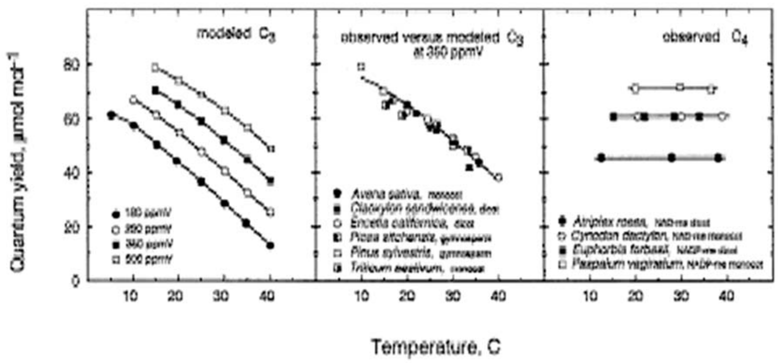
C4 plants have distinct and much less negative del 13C isotope ratios than C3 plants. It is a great tracer for distinguishing diets among C3 and C4 grasses. C4 grasses are also deemed to have higher water use efficiencies than C3 grasses because they have lower stomatal conductances and achieve lower Ci/Ca ratio (0.7 for C3 grasses and 0.4 for C4 grasses)

C_3 vs C_4 Photosynthesis: Light Use Efficiency, CO_2 and Temperature



Ehleringer et al, Oecologia

Comparative EcoPhysiology

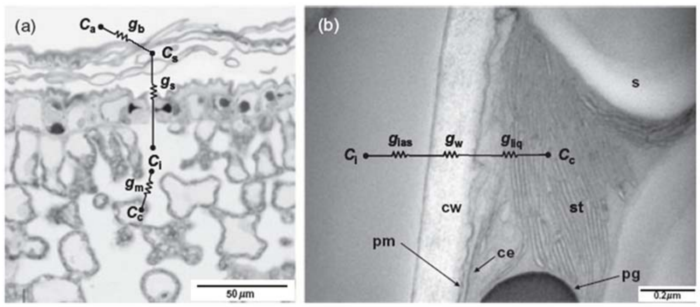
	C_3	C_4	CAM: day	CAM: night
internal [CO2]	0.7 Ca	0.4 Ca	0.5 Ca	?
Krantz ananatomy	NO	YES	Succulent	
carboxylase	RuBP	PEP	RuBp	PEP
photorespiration	YES	NO		
Fixation product	PGA	C_4 acids	PGA	C4 acids
CO2 compensation pt	30 -80 ppm	< 10 ppm	50 ppm	< 5 ppm
optimum temperature	15-30 C	25-40C	35 C	
Max Ps (mmol m^{-2} s^{-1})	14-40	18-55	6	8
Response at full sunlight	saturated	Linear	Saturated	
Enhancement in low O_2	yes	no	yes	No
Quantum req.	15-22	19		
Quantum yield	0.052	0.064		
Carbon isotope fractionation, per mill	-26 (-23 to -33)	-14	-30 to -10	-30 to -10

Adapted from Jones, 1992

Resistance -Analog

$$A = \frac{(C_a - C_c)}{r_{leaf} + r_{mesophyll} + r_{chloroplast}} =$$

$$g_b(C_a - C_s) = g_s(C_s - C_i) = g_m(C_i - C_c)$$



Flexas et al 2008, Plant, Cell, Environ

Leaf Photosynthesis

$$A = V_c - 0.5 V_o - R_d$$

Leaf photosynthesis (*A*) is a function of:

Rate of carboxylation (*Vc*), which is the minimum of the rates associate with regeneration of RuBP by electron transport and the saturation of RUBISCO by CO_2,

Rate of oxygenation (*Vo*, photorespiration) which is governed by the competition between CO_2 and O_2 for RUBISCO

Rate of dark respiration (*Rd*)

(all have units of μmol m^{-2} s^{-1}).

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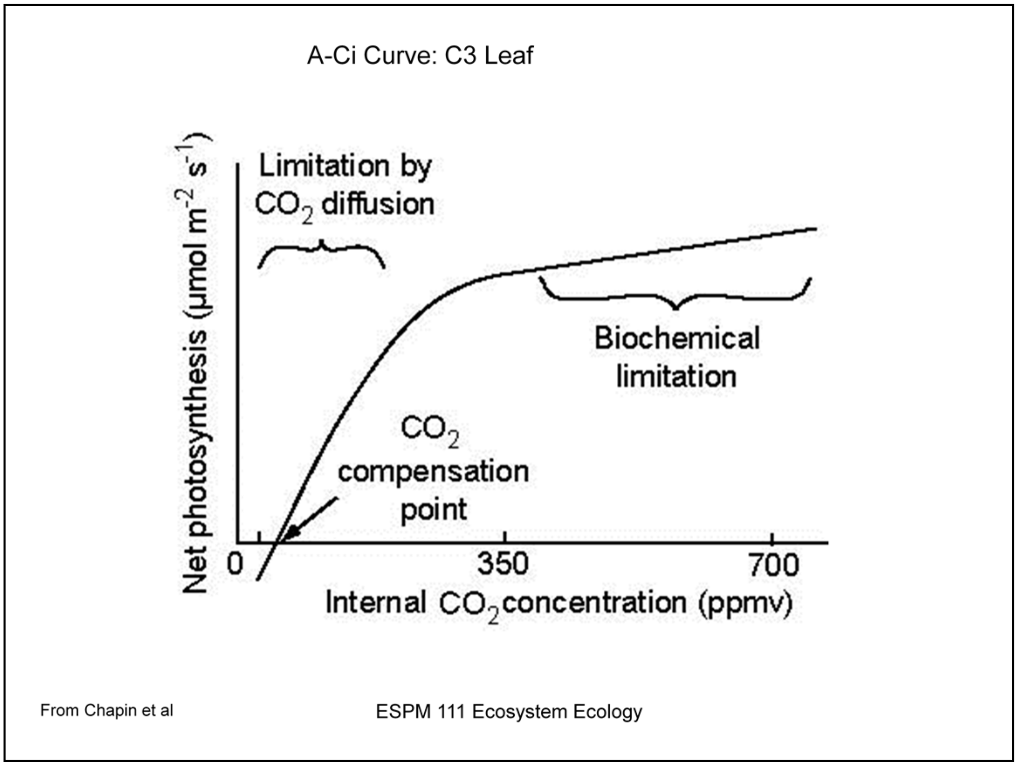
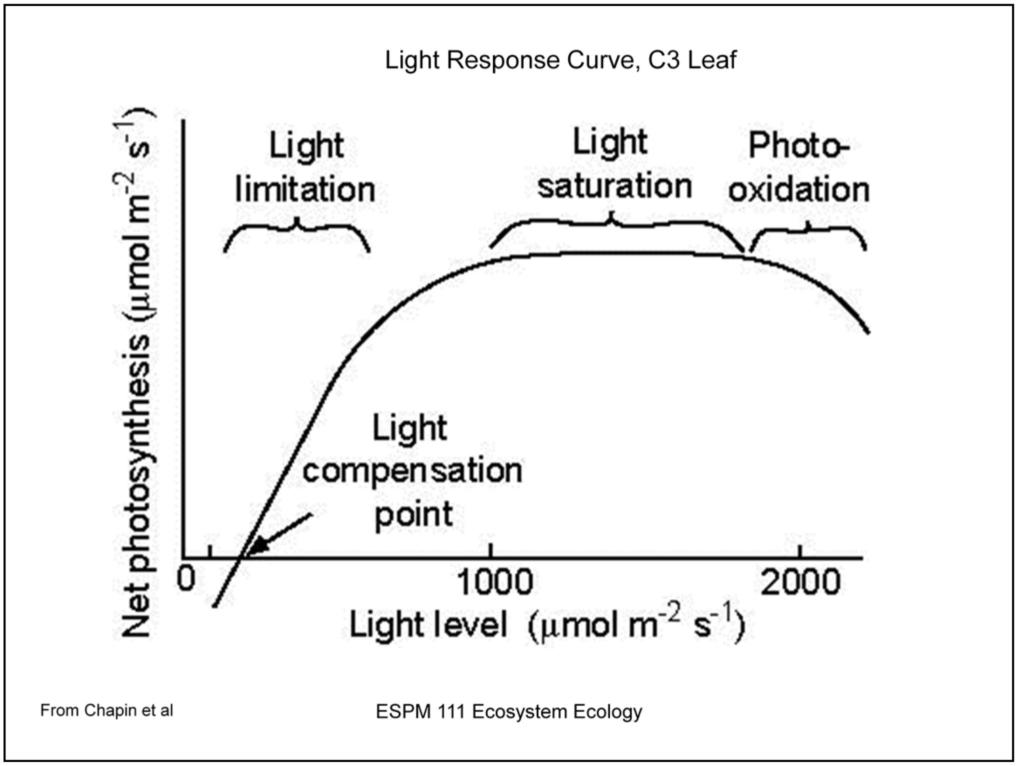
Vo/Vc is 0.27 at ambient conditions, so for each carboxylation, there is 0.13 (0.5 times 0.27 = Vo/Vc) oxygenations

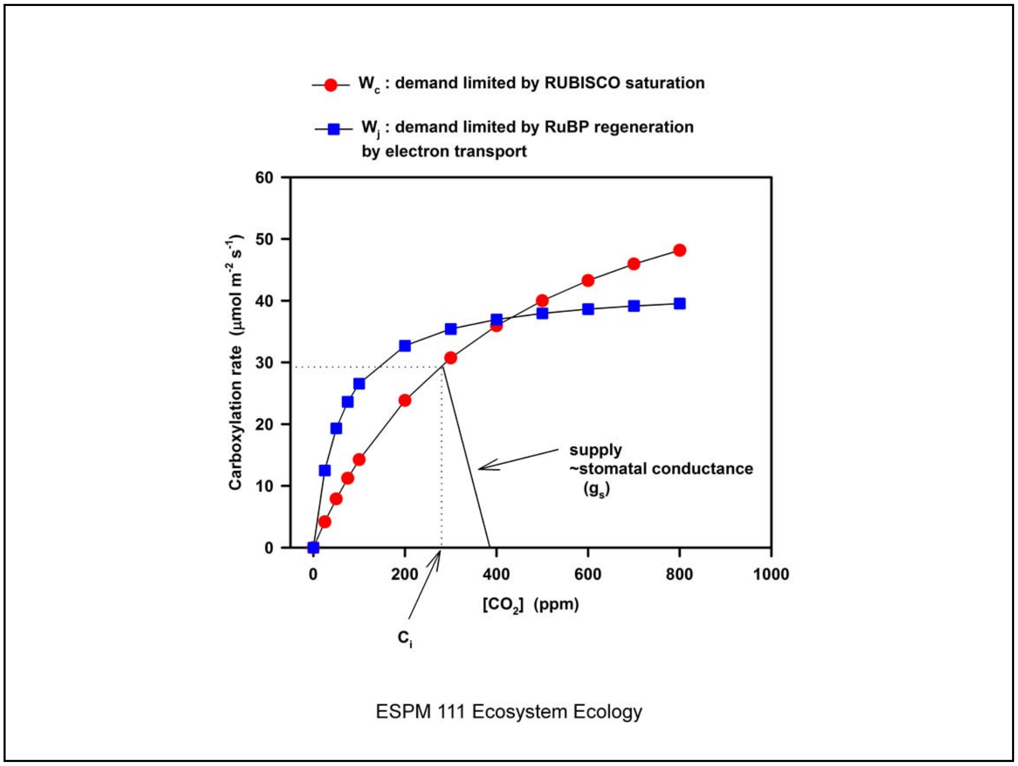


Non linear response curve to rising CO2. Note with certain levels of CO2 photosynthesis will start to saturate. Ci is about 0.7 Ca so Ci ~ 350 is at about 500 ppm Ca



Photosynthesis of leaves also saturate with light. The saturation level depends in part to leaf exposure and the photosynthetic machinery invested. Shaded adapted leaves, deep in a canopy receive low light levels (10% of full sun) so they don't invest in thick Ps machinery. So the saturation level is lower than a fully sun leaf.

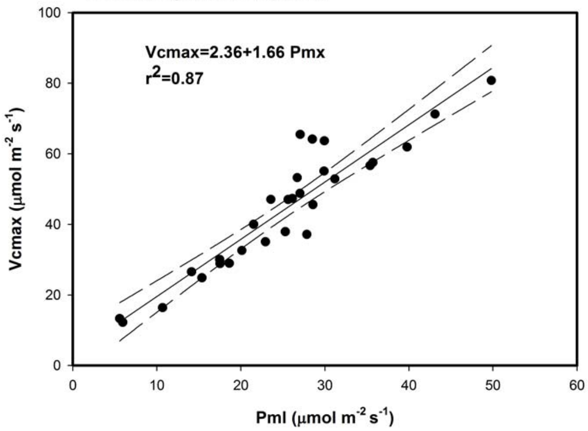
From chapin



Actual leaf ps rates is a fight between supply and demand, in terms of light energy to drive RuBP regeneration by electron transport, or the saturation of Rubisco due to CO2 levels. Graphically we can also see how stomatal conductance changes with C3 and C4 leaves or how it may change with rising or lowering CO2. In practice stomatal conductance decreases (resistance increases) with increasing CO2

V_{cmax} scales with maximum photosynthesis at saturating light and ambient CO2, P_{ml}

Wohlfarht 1999
mountain grassland species



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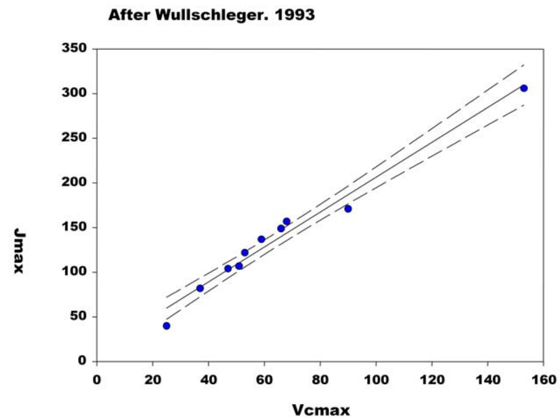
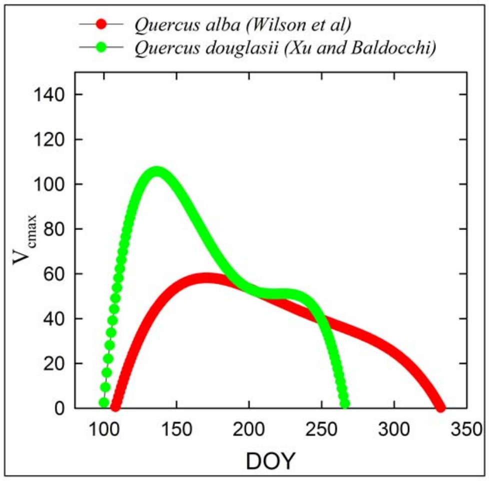
Maximum rate of Carboxylation, V_{cmax}, scales with maximum rate of electron transport, J_{max}

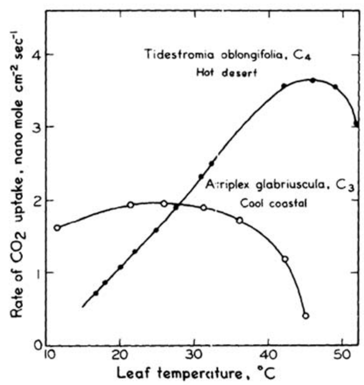


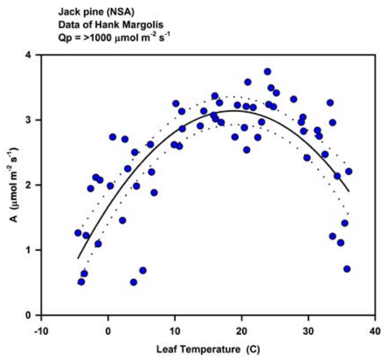
Seasonality of Model Parameters: e.g. Photosynthetic Capacity



Live Fast, Die Young
In Stressed Environments

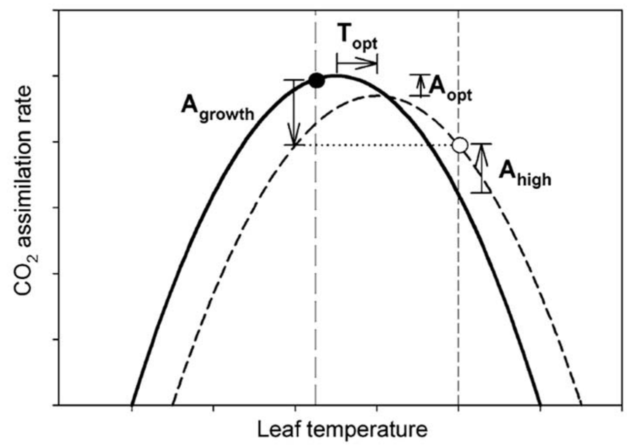
Photosynthesis and Temperature





Berry and Bjorkman 1980, Ann Rev Plant Physiol

Photosynth Res (2014) 119:89–100



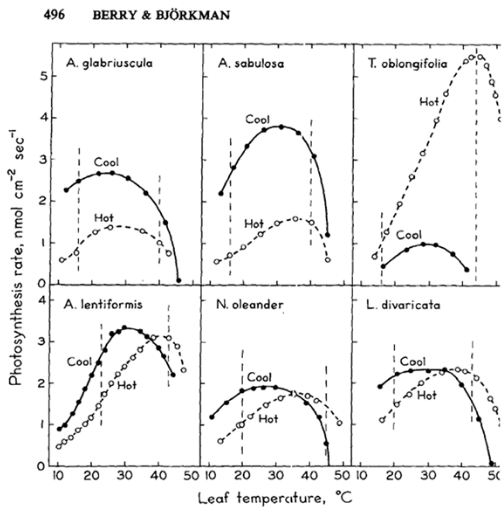
Way and Yamori, 2014 Photosynthetic Research

Stress Physiology

- *Adaptation is a response to long-term changes* which result in inheritable genetic alterations. These alterations are stable and will remain in the population over generations.
- *Acclimation* is a response induced by an environmental change which causes a phenotypic alteration over a single generation time without any compositional change in the genetic complement
  - Stomata close to limit water loss
  - Temperature optimum shifts with warmer temperatures
- Tolerance
  - Blue oaks are able to photosynthesize despite super severe water deficits (below -5.0 Mpa)
- Avoidance
  - CA grasses adopt annual life strategy. Survive dry summer in the form of dessicated seeds
  - Blue oaks develop deep roots that tap into the ground water

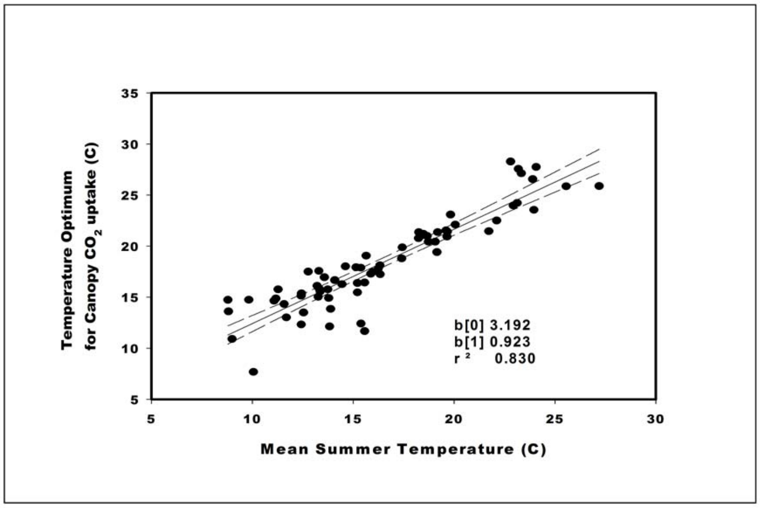
- Huner et al 1993 Photosyn Res

P_s and Temperature Acclimation



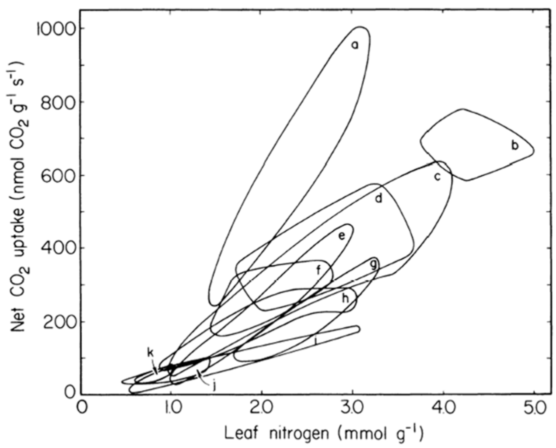
Berry and Bjorkman 1980, Ann Rev Plant Physiol

GPP: Acclimation with Temperature



Analysis of E. Falge

Photosynthesis and Leaf Nitrogen



Field and Mooney, 1986

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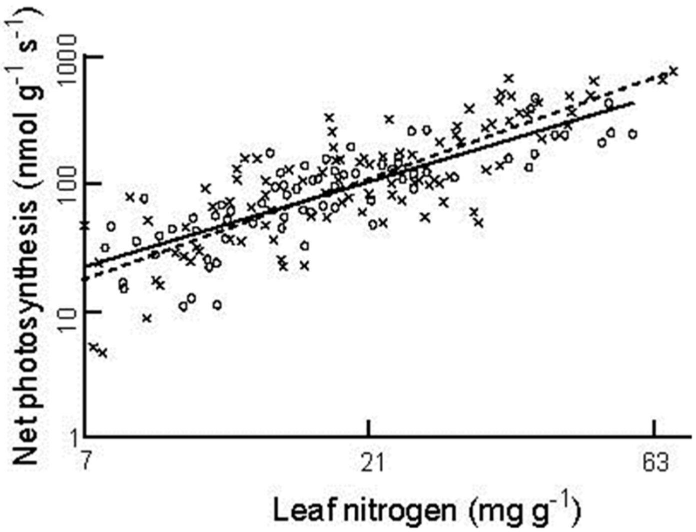
Photosynthesis scales with Nitrogen. One of the first papers on this topic, circa 1986, Field and Mooney



Reich et al 1997 PNAS

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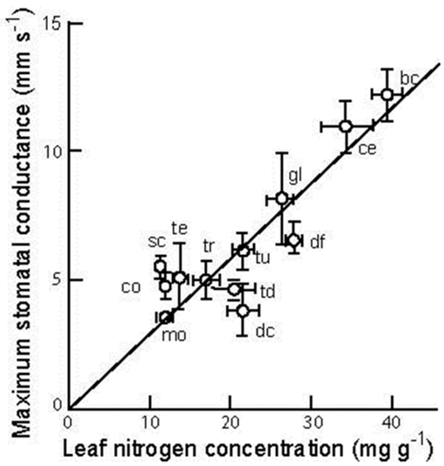
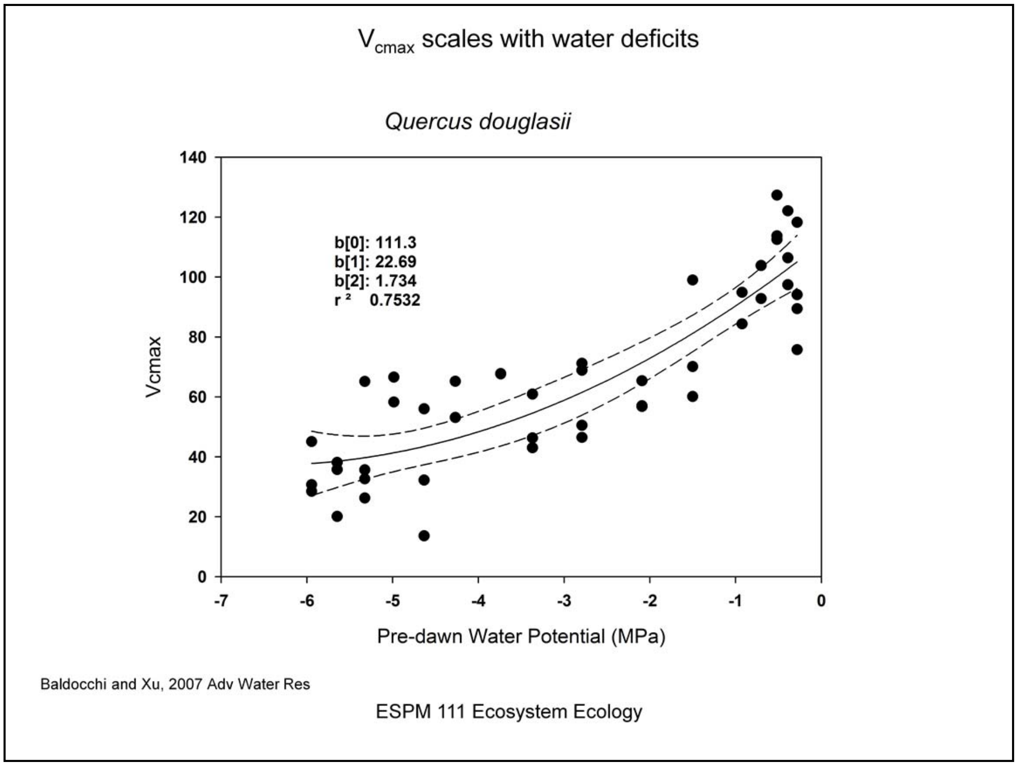
More data on photosynthesis and nitrogen. Power of big data, data mining and scaling laws. This figure follows a log log pattern

Stomatal conductance adjusts to match photosynthetic capacity (or vice versa)



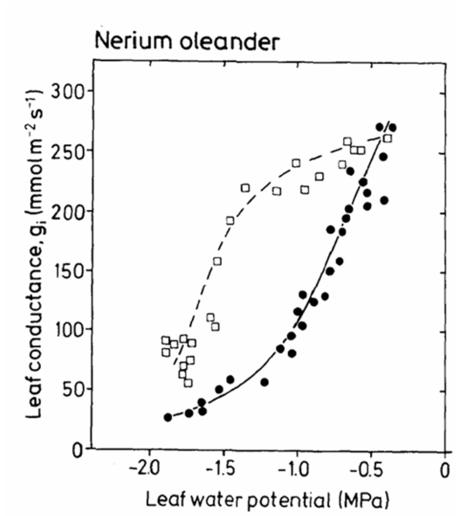
Schulze et al 1994 Ann Rev Ecol

Stomatal and photosynthesis, scale, so does stomatal conductance and leaf N. Hence we can expect higher transpiration rates with fertilized crops than more nutrient poor native vegetation.



Photosynthetic capacity decreases with drought, measured in terms of pre dawn water potential

Stomatal conductance and water deficits



Schulze 1986 Ann Rev Plant Physiol

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Soil water deficits impose stomatal closure.

Summary Points

- Leaf photosynthesis involves a set of light and dark reactions.
- The light reactions involve the harvesting of sunlight by chlorophyll and the transfer of electrons to the produce of biochemical energy compounds adenosine triphosphate (**ATP**) and nico-adenomine di-phosate (**NADPH**) via the process called photophosphorylation.
- The energy contained in molecules ATP and NADPH is subsequently used in the dark reactions to drive the photosynthetic carbon reduction cycle, or Calvin Cycle.
- There are three photosynthetic pathways, C3 (the most common), C4 and CAM.
- Photorespiration, due to the competitive affinity for CO2 and O2 by the enzyme RUBISCO, is an attribute of C3 photosynthesis.
  - This leads to its lower efficiency than C4 photosynthesis
  - C4 plants circumvents this inefficiency by using a different enzyme to carboxylze CO2 (PEP carboxylase) and by minimizing the diffusion of O2 deep in the leaf with its unique leaf anatomy (bundle sheaths).
- Rates of photosynthesis achieved by a leaf is a balance between the supply and the demand for carbon dioxide. The supply is related to the CO2 concentration in the air and its diffusion through the leaf boundary layer and stomata. The demand is controlled by the Michaelis-Menton kinetic reactions that are a function of CO2 at the chloroplast.
- Rates of photosynthesis are a function of light, temperature, CO2, moisture, leaf nutrition, and phytotoxics.