Carbon Input to Ecosystems

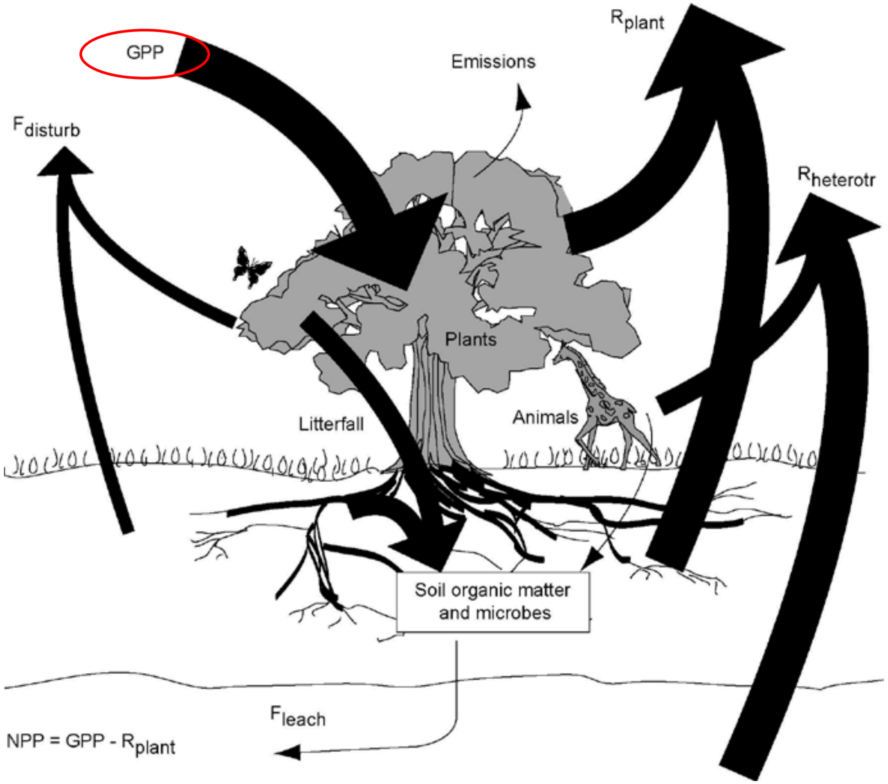
- Objectives
  - Carbon Input
    - Leaves
      - Photosynthetic pathways
    - Canopies (i.e., ecosystems)
  - Controls over carbon input
    - Leaves
    - Canopies (i.e., ecosystems)
  - Terminology
    - Photosynthesis vs. net photosynthesis vs. gross primary production vs. etc., etc., etc.

Carbon Input to Ecosystems

- Carbon makes up ~1/2 of organic matter on Earth (H and O account for most of the rest)
  - Carbon (≈ Biomass) = **Energy currency in ecosystems**
    - **Largely the same processes govern entry, transfers and losses of both C & energy**
- Photosynthesis provides carbon/energy that drives nearly all biotic processes
  - Controlled by:
    - Leaf: Availability of water, nutrients, temperature, light, CO_2
    - Ecosystem: Growing season length, leaf area
    - Both ultimately controlled by availability of soil resources, climate, and time since disturbance

Carbon Input to Ecosystems

- Carbon cycles into, within, and out of ecosystems
  - Like H_2O, but different controls, processes, & pathways
    - Start by focusing on ecosystem C input (i.e., GPP)

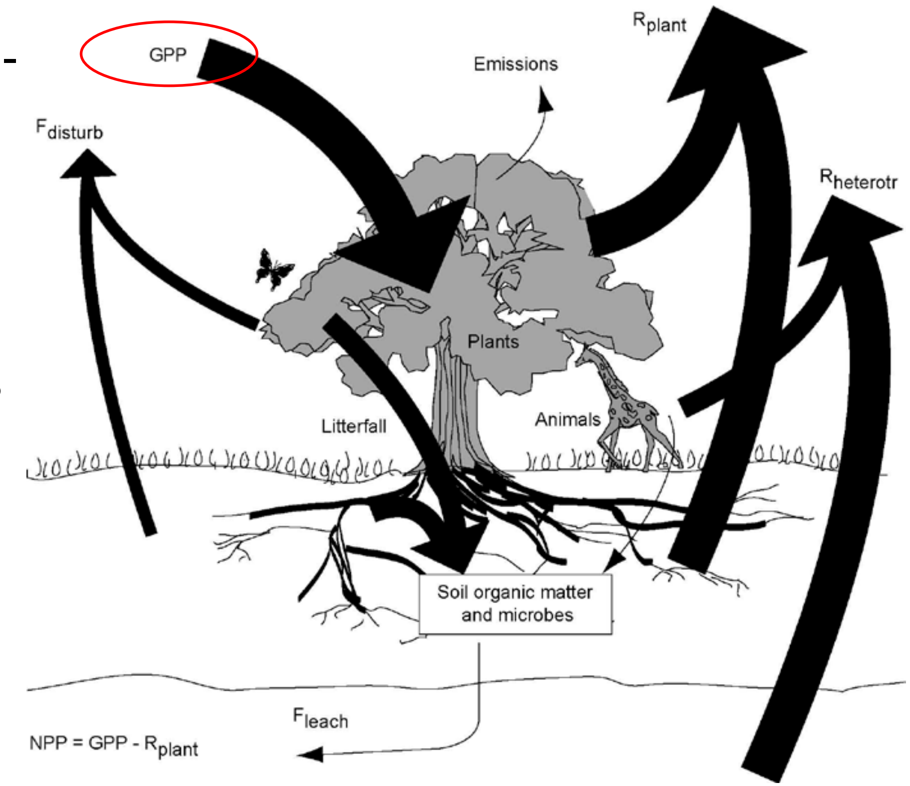


Carbon Input to Ecosystems

- Gross Primary Productivity (GPP) = Net photosynthesis at the ecosystem scale
  - Net photosynthesis = Gross photosynthesis – [R_{leaf} during the day + photorespiration]
    - Gross Photosynthesis = total CO_2 Assimilation ≠ GPP
- GPP - Autotrophic Respiration = Net Primary Production (NPP)
  - NPP is the net accumulation (or loss) of carbon by primary producers that is used to drive ecosystem processes

Carbon Input to Ecosystems

- C enters via photosynthesis
  – Gross Primary Production (GPP)
    - Net photosynthesis (Gross photo - R_{leaf} during the day)
  1. Accumulates in ecosystems (C sequestration) as: (a) plant biomass; (b) Microbial biomass &/or SOM; or (c) animal biomass
  2. Returned to the atmosphere via (a) respiration (*R*; autotrophic or heterotrophic); (b) VOC emissions; or (c) disturbance
  3. Leached from or transferred laterally to another ecosystem



Carbon Input to Ecosystems

- <u>Photosynthesis is most efficient when CO_2 supply matches CO_2 demand of biochemical reactions</u>
  - Physical limitation: delivery of CO_2 to leaf by diffusion
    - Stomatal conductance & tradeoffs with H_2O availability
  - Biochemical limitation: carboxylation rate
    - Light limitation
      - Solar radiation provides energy source for photosynthesis
    - Enzyme limitation
      - Enzymes use CO_2 and energy from solar radiation to “fix” inorganic CO_2 into organic form

Carbon Input to Ecosystems

- Photosynthesis is comprised of 2 major sets of reactions:
- Light-harvesting reactions (light dependent)
  - Photosystems I and II convert light energy into temporary chemical energy
- Carbon fixation reactions (light independent)
  - Rubisco uses chemical energy to convert CO_2 into sugars during carboxylation
    - More permanent form of chemical energy that can be stored, transported, or metabolized

Carbon Input to Ecosystems

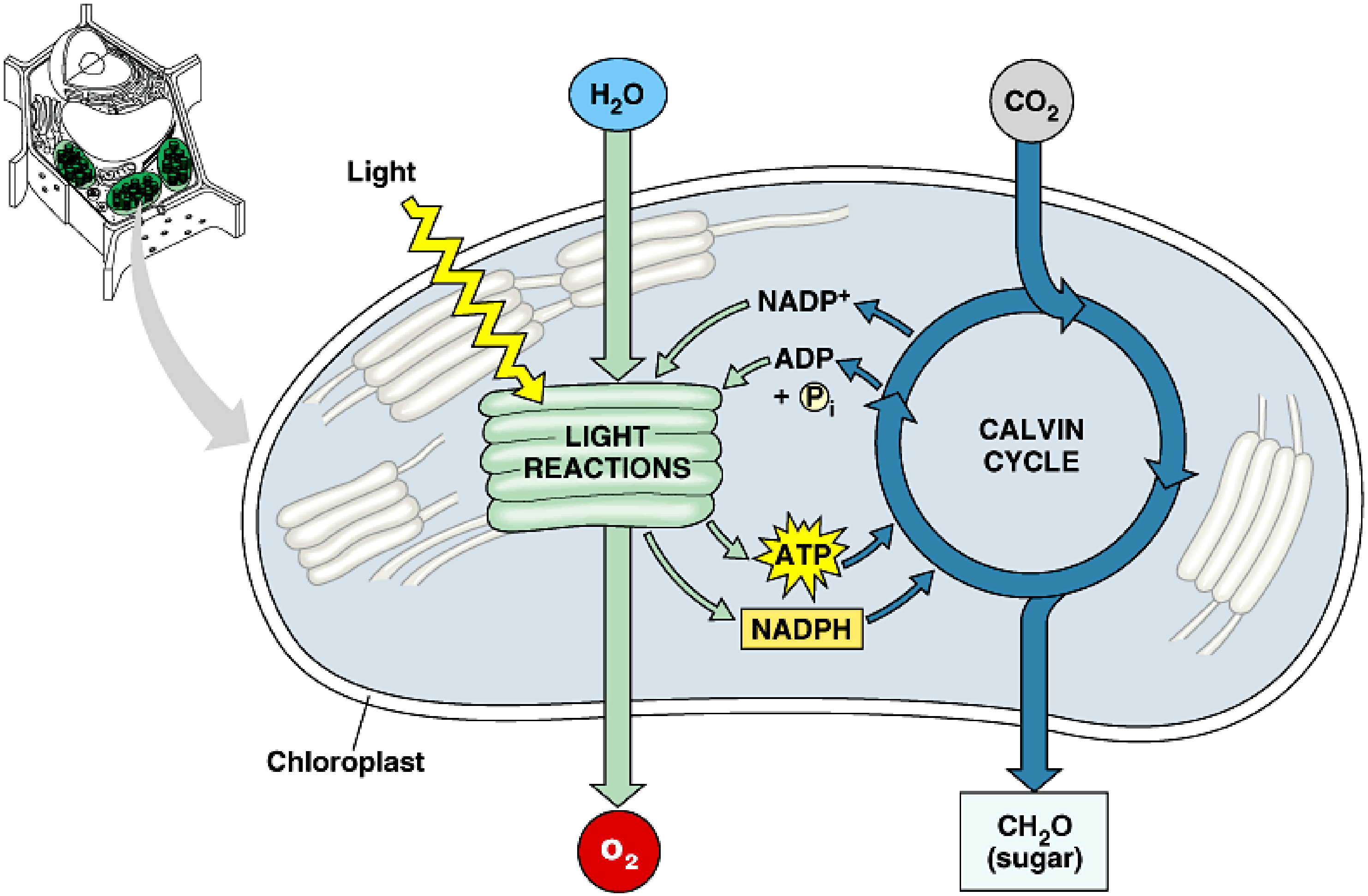
- 3 major photosynthetic pathways:
  - C3 photosynthesis
    - ~85% of species; ~80% of NPP
  - C4 photosynthesis
    - ~3% of species; ~20+% of NPP; ~1/3 of ice-free land
    - Tropical grasslands and savannas; salt marshes
    - Warm, high light, and/or dry environments
  - CAM photosynthesis
    - Not very common; Succulents, epiphytes; Plants adapted to extremley dry conditions
  - *C3 photosynthesis is the fundamental mechanism by which carbon enters ALL terrestrial ecosystems*

Carbon Input to Ecosystems

- C3 photosynthesis
  - In chloroplasts in the mesophyll cells
    - Light harvesting reaction
      - Visible light (~40% of incoming solar radiation)
      - O_2 is a "waste product" when H_2O molecules are split
      - Limited by supply of light
    - Carbon fixation reaction (carboxylation)
      - Reduction of CO_2 to 3-C sugars (phosphoglycerate)
      - Limited by products of light harvesting reaction, enzyme Rubisco (nutrients), & CO_2 supply (i.e., internal CO_2 concentration)

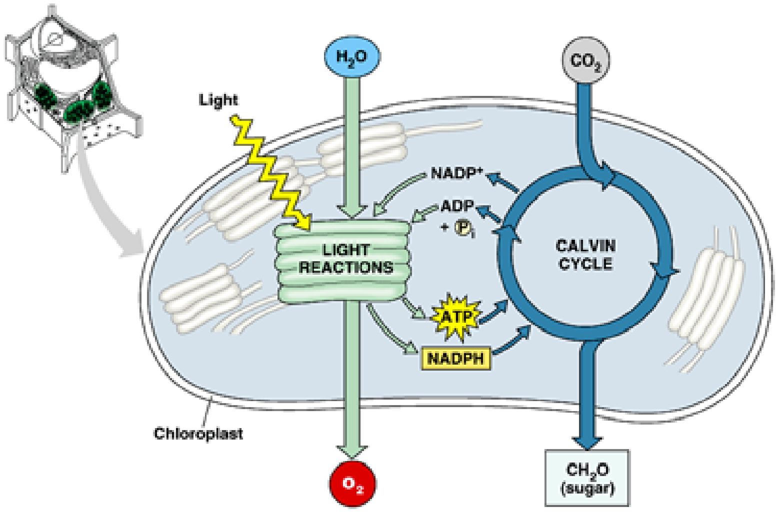
Simple overview of C3 photosynthesis

C3 mesophyll cell

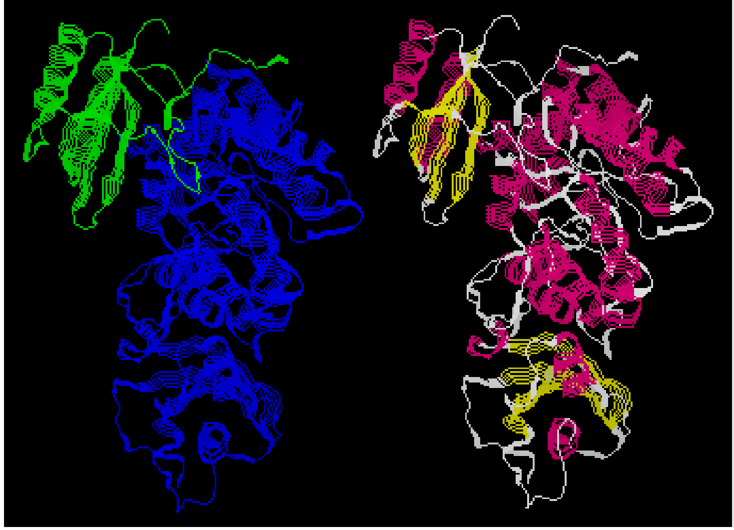


Carbon Input to Ecosystems

- C3 photosynthesis highlights
  - Large N requirement for enzymes (~50% of foliar N)
  - Dependence on products of light-harvesting reaction (which is limited by irradiance)
  - Frequently limited by CO_2 supply to chloroplasts



Carbon Input to Ecosystems

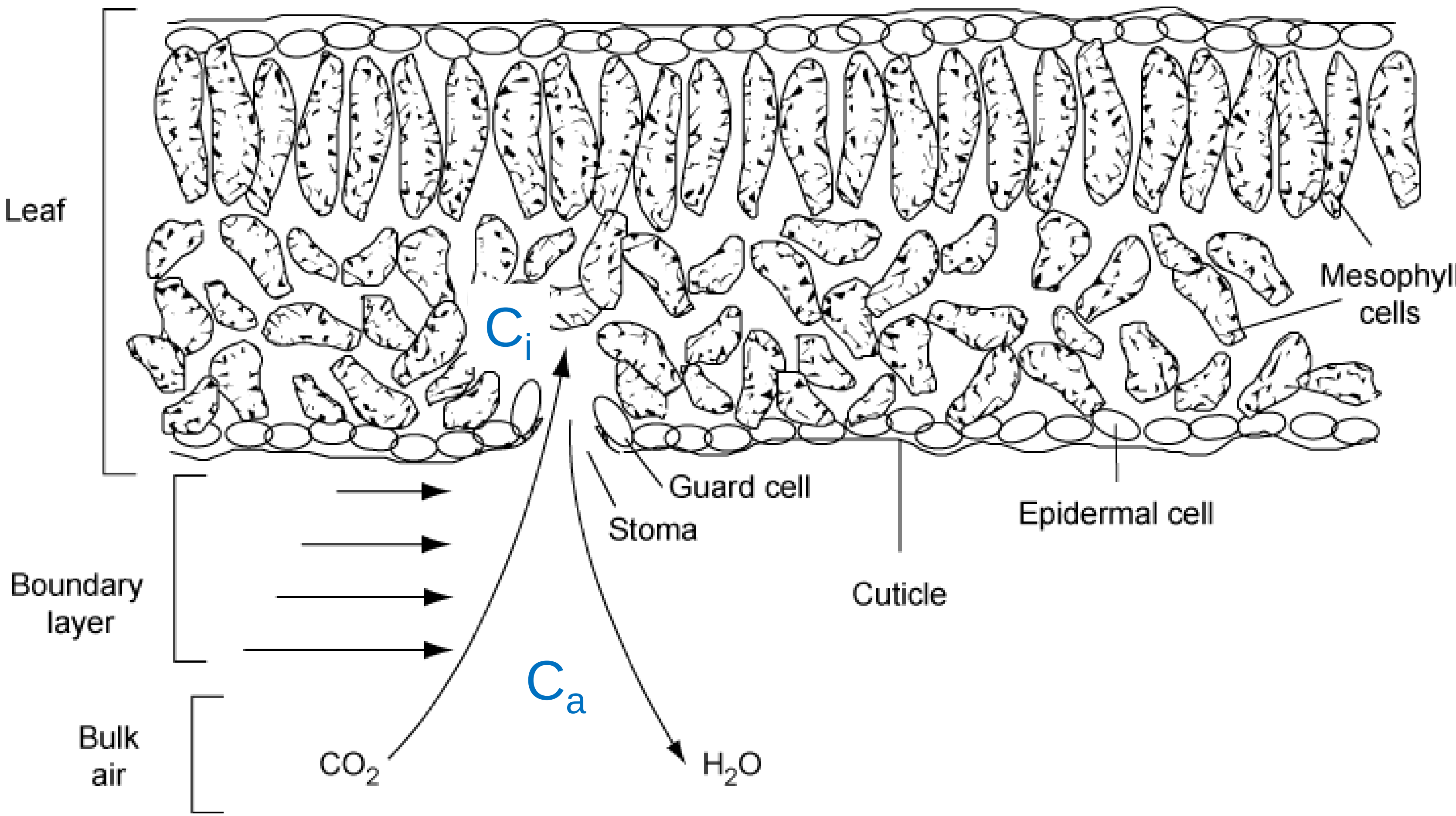


- Rubisco can gain or lose C???
- Carboxylase
  - Reacts with CO_2 to produce sugars (carbon gain)
- Oxygenase (≈photorespiration)
  - Reacts with O_2 to convert sugars to CO_2 (carbon loss)
    - Photorespiration uses 20-40% of carbon fixed during photosynthesis in C3 plants!!!
  - Why?
    - Early Earth had low O_2 and high CO_2 concentrations
    - Regenerates ADP and NADP for light reactions - Safety valve
      - Keeps light harvesting reaction going when CO_2 is limiting
      - Limits presence of O_2 radicals

Carbon Input to Ecosystems

- **GPP =** Net photosynthesis
  - = Total CO_2 assimilation – (foliar respiration in day + photorespiration)
  - **=** Net rate of C gain in leaves
  - Overall efficiency of 1-2% of incoming solar radiation
    - Often limited by supply of CO_2, and/or light

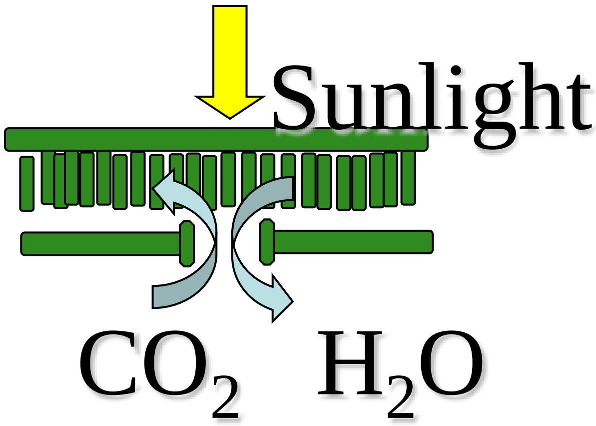
Carbon Input to Ecosystems



- Photosynthesis is a diffusion process
- Assimilation (*A*) ≈ $(C_a - C_i) * g_s$ (A ≈ Driving force * Conductance)

Carbon Input to Ecosystems

- Photosynthesis is a constant compromise / tradeoff between H_2O loss and CO_2 uptake
  - Transpiration vs. Photosynthesis
    - Photosynthesis: 1 H_2O molecule for every CO_2 molecule
    - Transpiration: 400 molecules of H_2O lost for every molecule of CO_2 absorbed
  - Stomata regulate this tradeoff



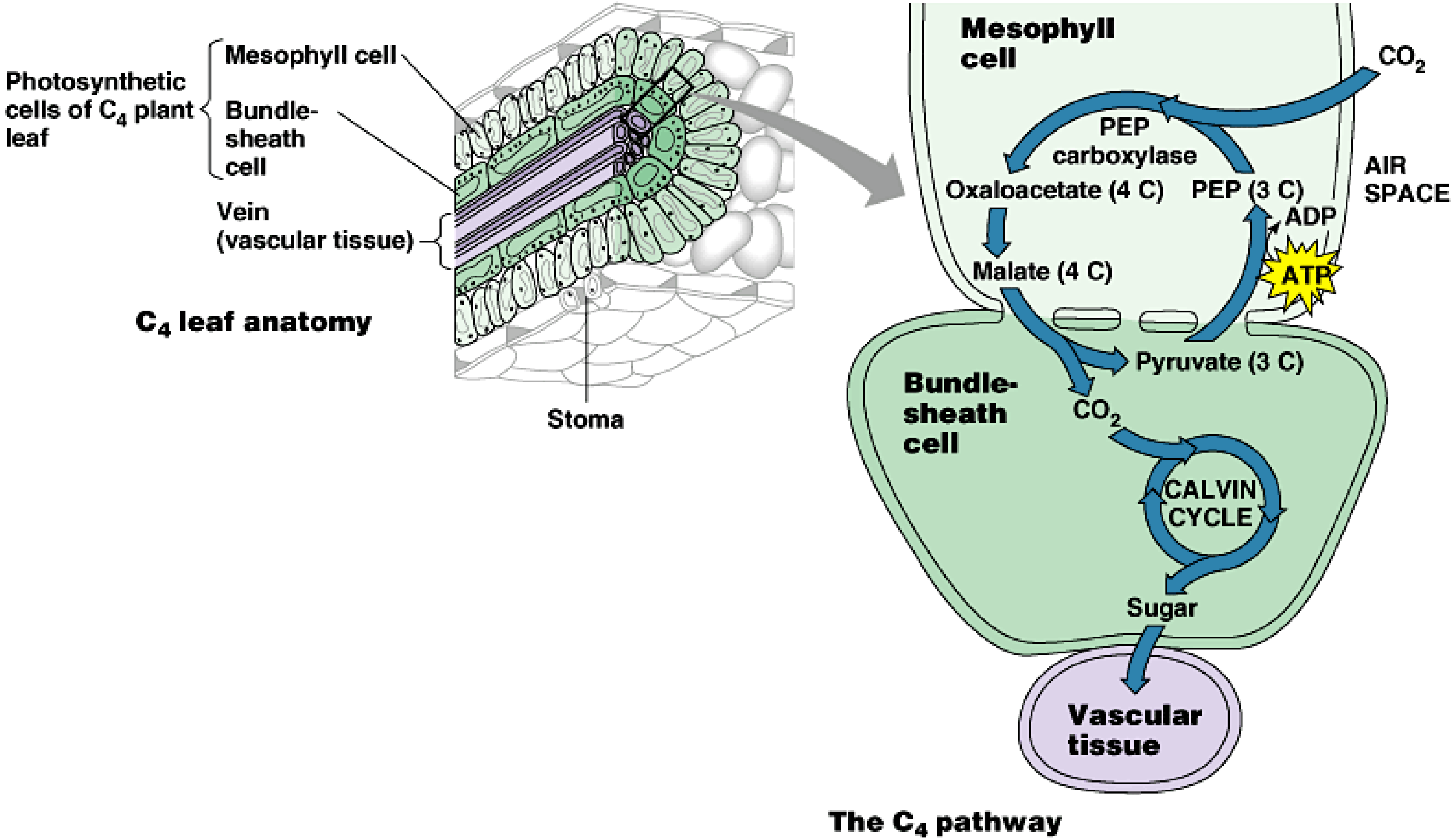
$$6CO_2 + 6H_2O + energy \leftrightarrow C_6H_{12}O_6 + 6O_2$$

Carbon Input to Ecosystems

- C4 photosynthesis
  - C3 photosynthesis + an additional set of reactions
    - PEP carboxylase produces 4-C acid in mesophyll cells
      - Transported to bundle sheath cells
    - In bundle sheath cells, 4-C acid is decarboxylated (releases CO_2) and C3 photosynthesis occurs (Calvin Cycle)

  - *The major benefit of C4 photosynthesis is increased carboxylation under conditions that would otherwise favor photorespiration in C3 plants*

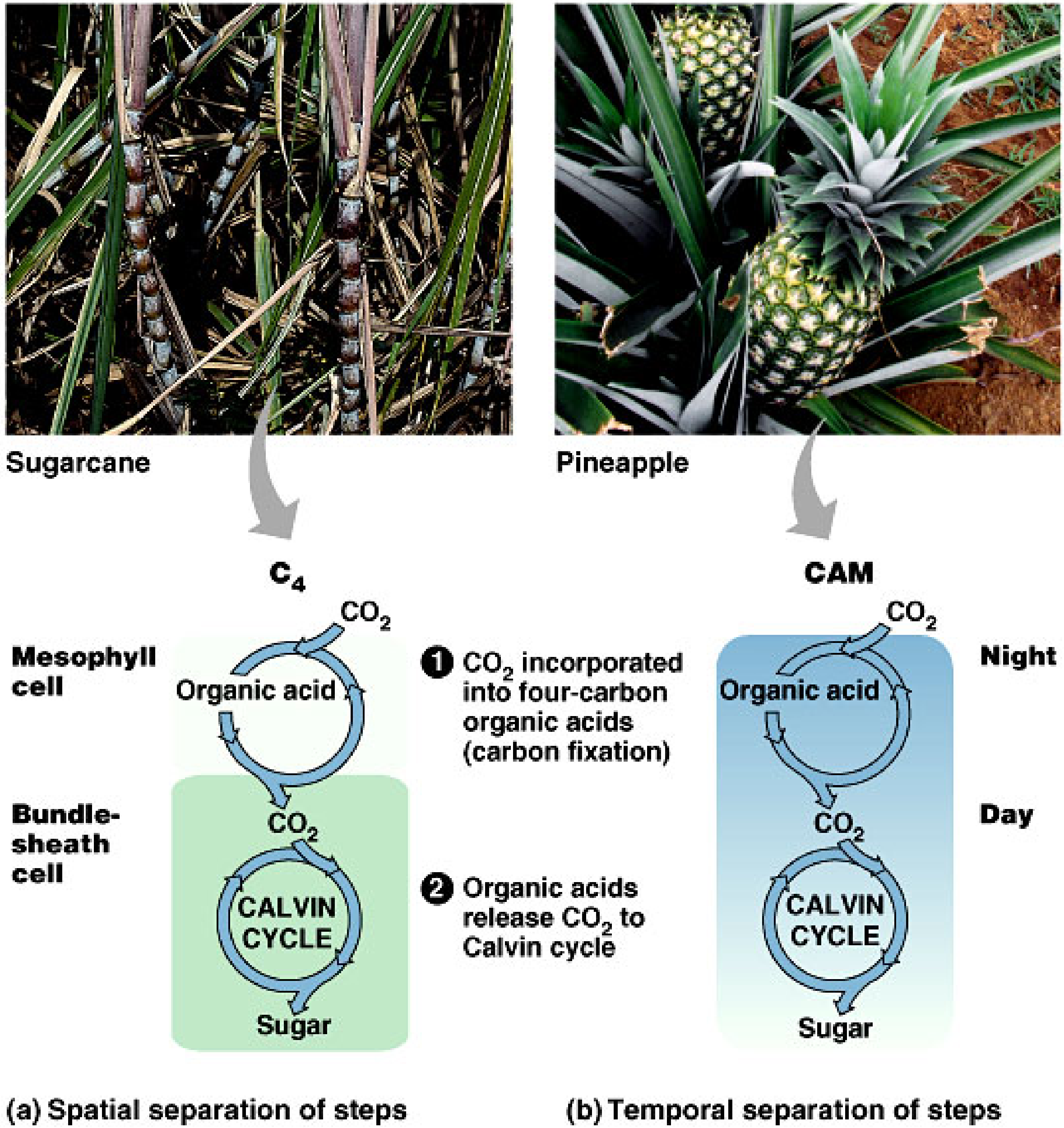
Overview of C4 photosynthesis



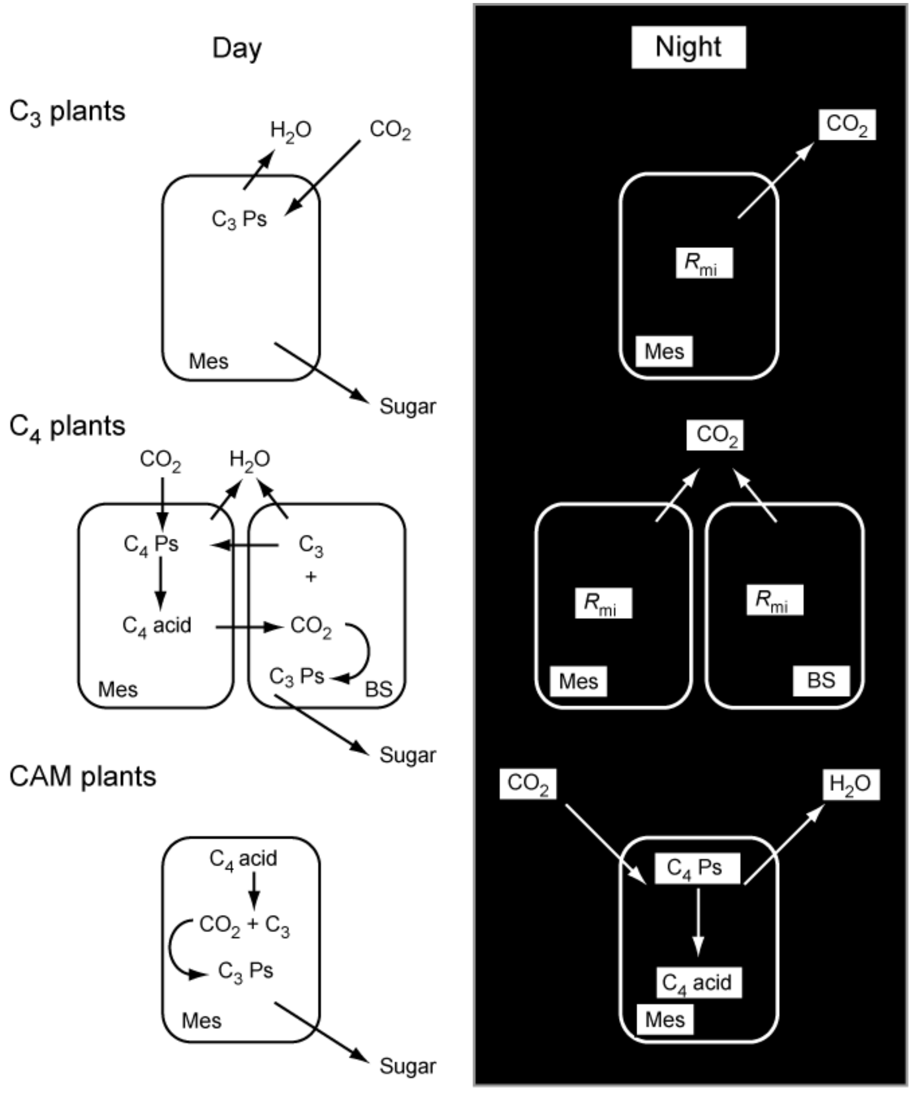
Carbon Input to Ecosystems

- C4 photosynthesis highlights
  - Concentrates CO_2 in bundle sheath cell where Rubisco fixes carbon
    - Increases the efficiency of Rubisco carboxylation
    - Greatly reduces photorespiration
    - Reduces the quantity of Rubisco (and N) required
  - PEP carboxylase is more efficient than Rubisco at drawing down C_i
    - Increases CO_2 gradient → CO_2 diffuse more readily → reduces water loss (stomata can be more closed)
  - Why aren’t all plants C4?
    - PEP requires 30% more energy to regenerate

Carbon Input to Ecosystems

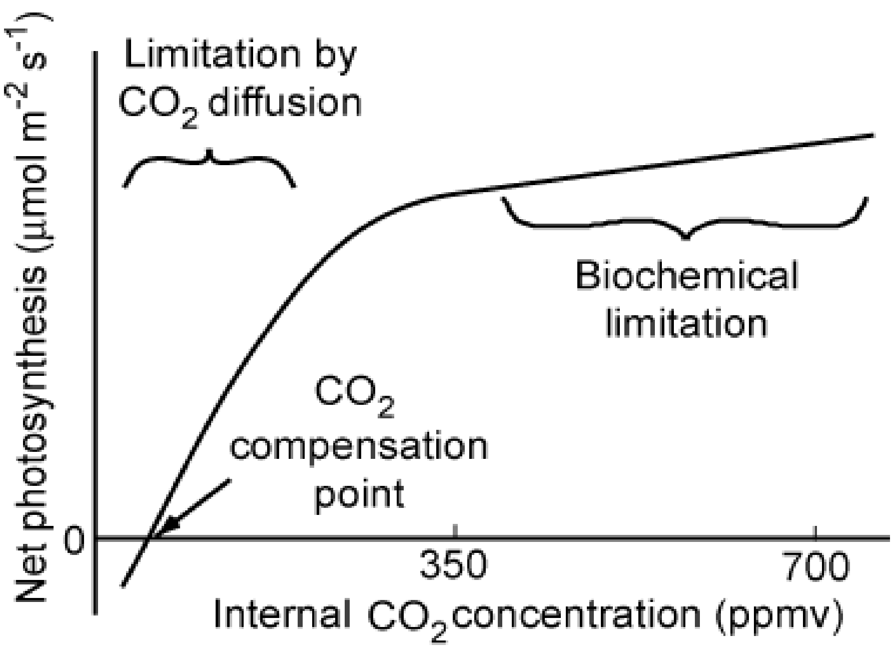


Carbon Input to Ecosystems



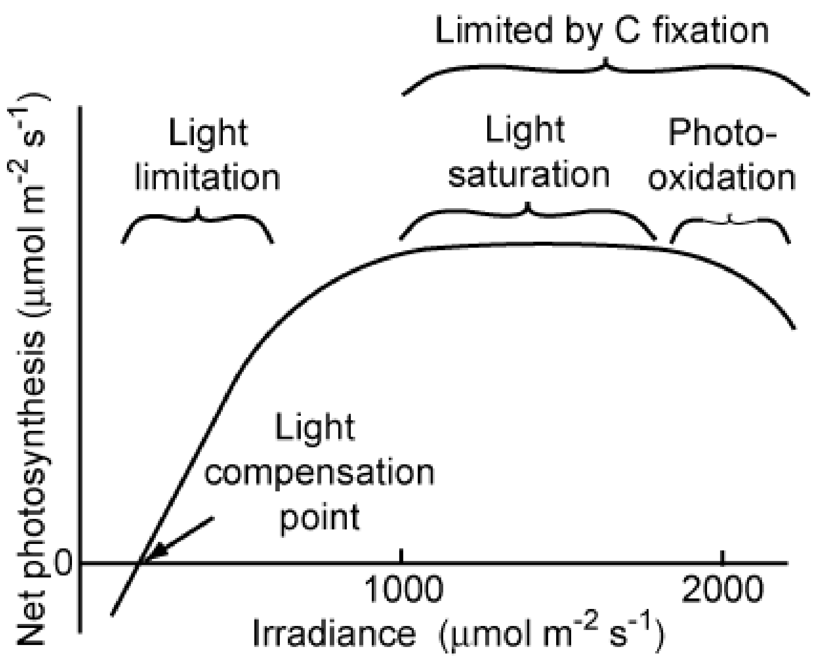
Carbon Input to Ecosystems

- Net photosynthesis by individual leaves
  - **Plants adjust components of photosynthesis so physical and biochemical processes co-limit**
    - Diffusion of CO_2 ≈ Capacity of Rubisco to fix CO_2
    - Largely a stomatal control at low CO_2
    - *A* also limited by light, nutrients (N), water, and temp. at high CO_2



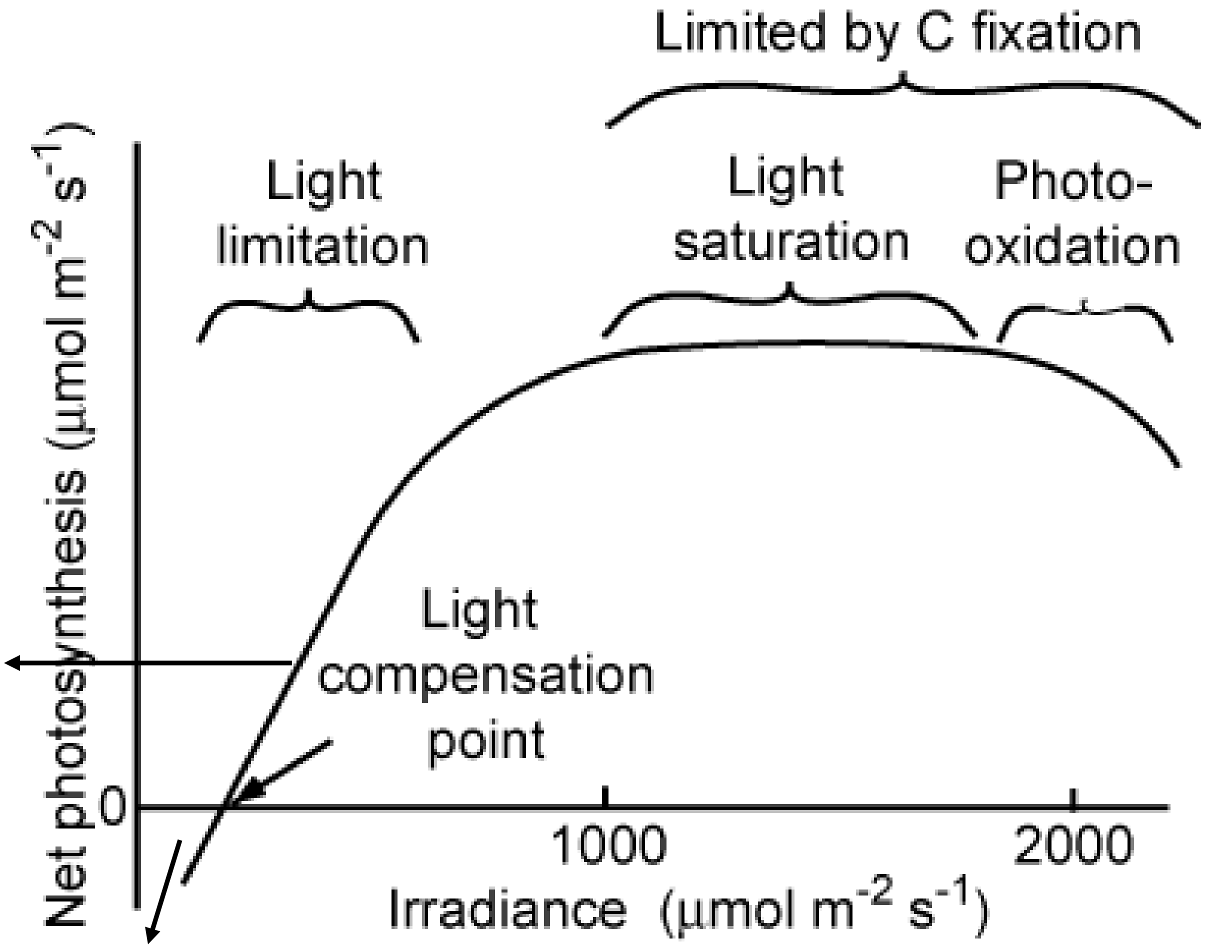
Carbon Input to Ecosystems

- Net photosynthesis by individual leaves
  - **Plants adjust components of photosynthesis so that light harvesting and CO_2-fixation reactions match**
    - Over minutes to hours, plants adjust stomatal conductance
    - Over course of leaf development, enzymes are distributed between light harvesting & carbon fixation based on prevailing env.



Carbon Input to Ecosystems

Light response curve of photosynthesis



Slope = quantum yield of photo. (Light Use Efficiency; LUE)

Net respiration (C source)

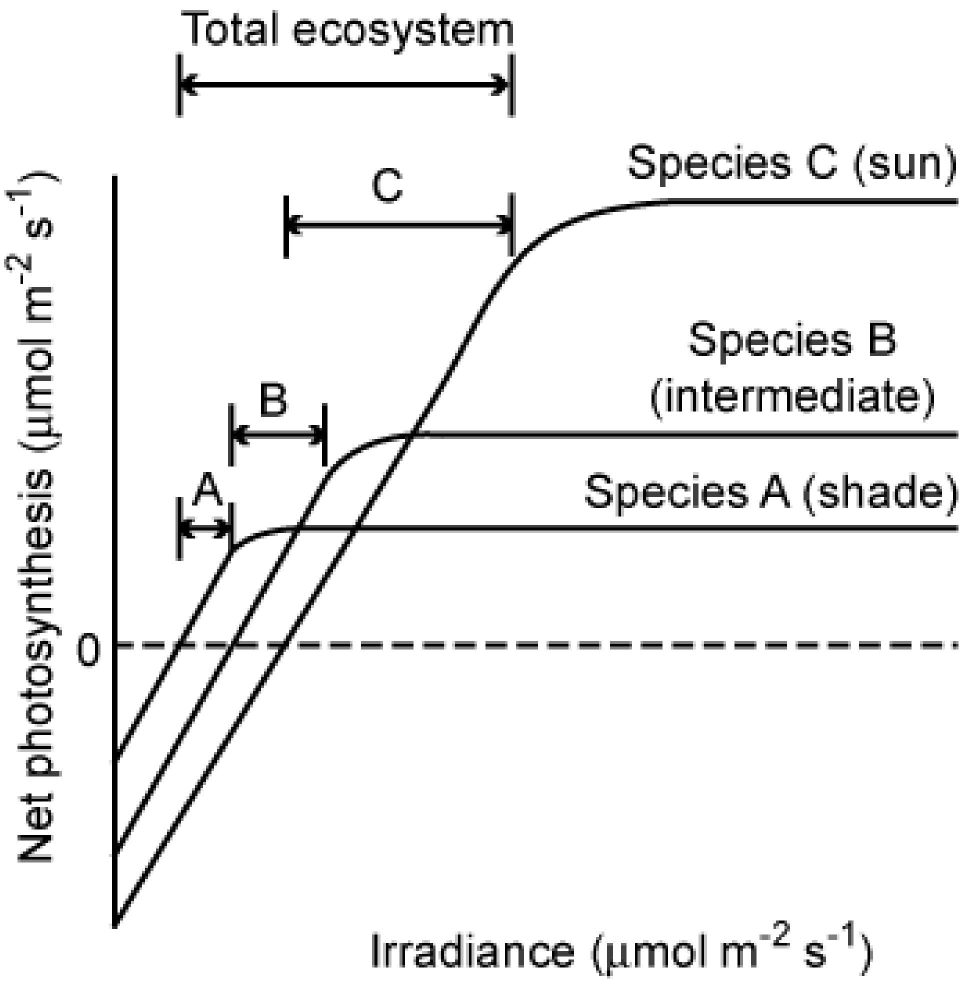
Carbon Input to Ecosystems

- LUE = *A* per unit of light received
  = initial, linear slope of light response curve
- Nearly constant in C3 plants at low light (~6%)
  – i.e., linear portion of light response curve is same in all C3 plants

Carbon Input to Ecosystems

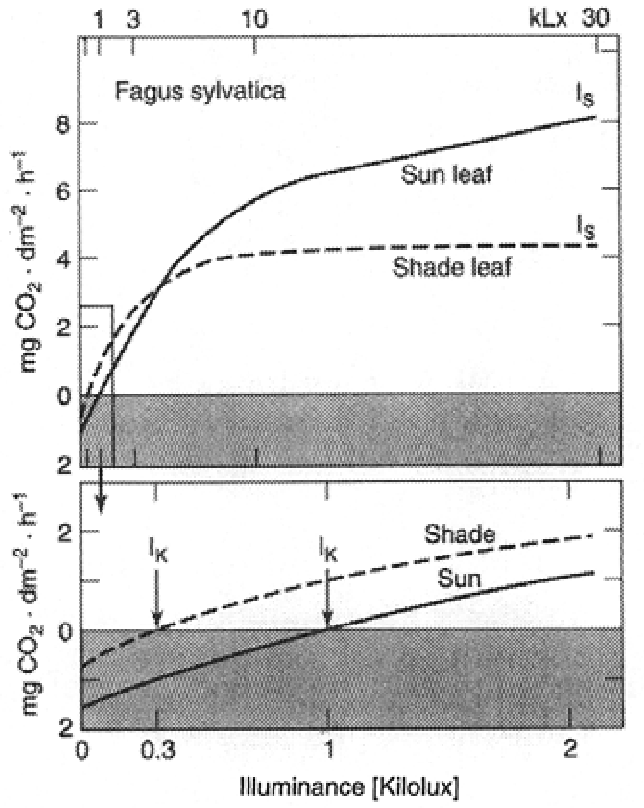
•Presence of multiple species increases range of light levels over which *A* responds linearly to light

•Important because of large decreases in incident light as you move down thru the canopy



Carbon Input to Ecosystems

- Within a given plant, sun vs. shade leaves are adapted to their light environments
  - Sun leaf takes longer to reach LCP, but has higher LSP
  - Shade leaf reaches LCP earlier, but has lower LSP

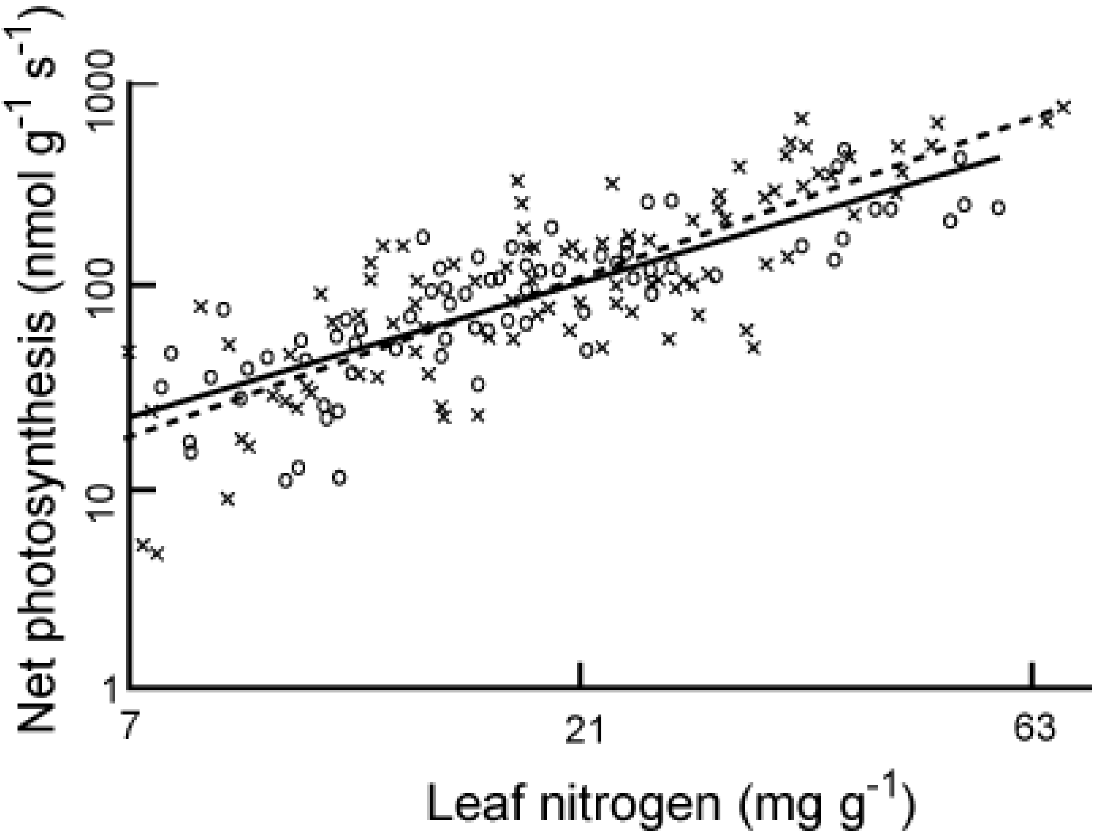


Carbon Input to Ecosystems

- Photosynthetic capacity (A_{max})
  - *A* per unit leaf mass under ideal conditions
    - C gain potential per unit investment in leaf biomass
  - 10 to 50-fold difference across species
    - Little to nothing to do with light availability

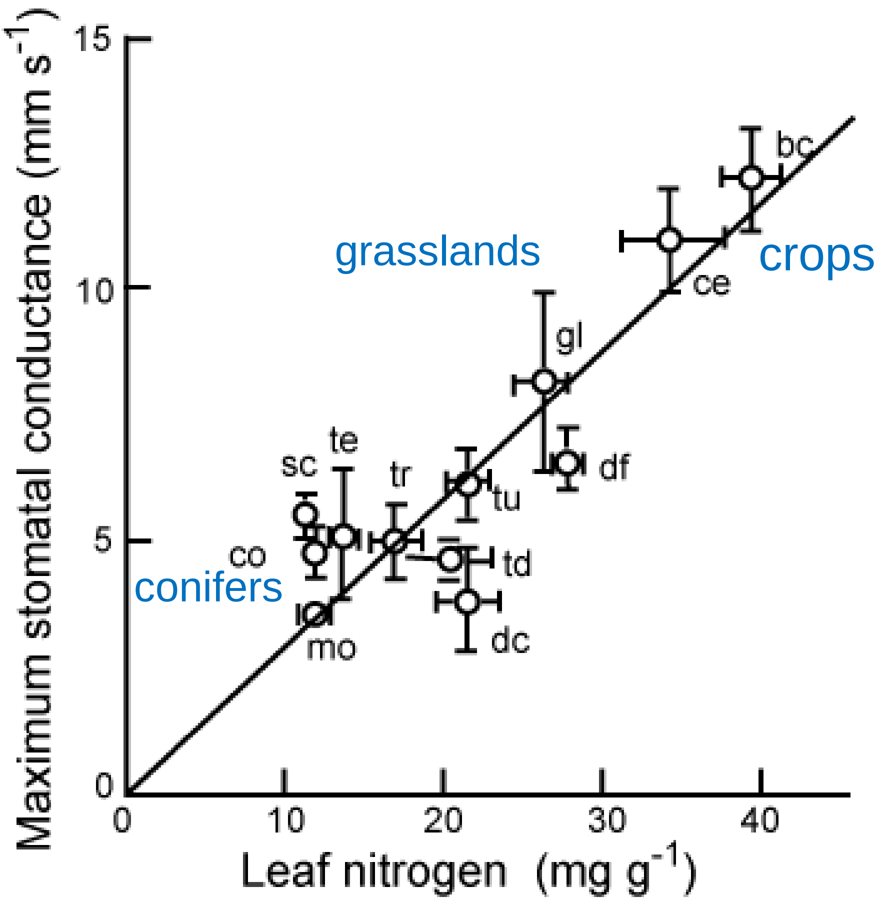
Carbon Input to Ecosystems

- Photosynthesis correlates strongly with leaf N content
- Why?
  - ~50% of foliar N is in photosynthetic enzymes



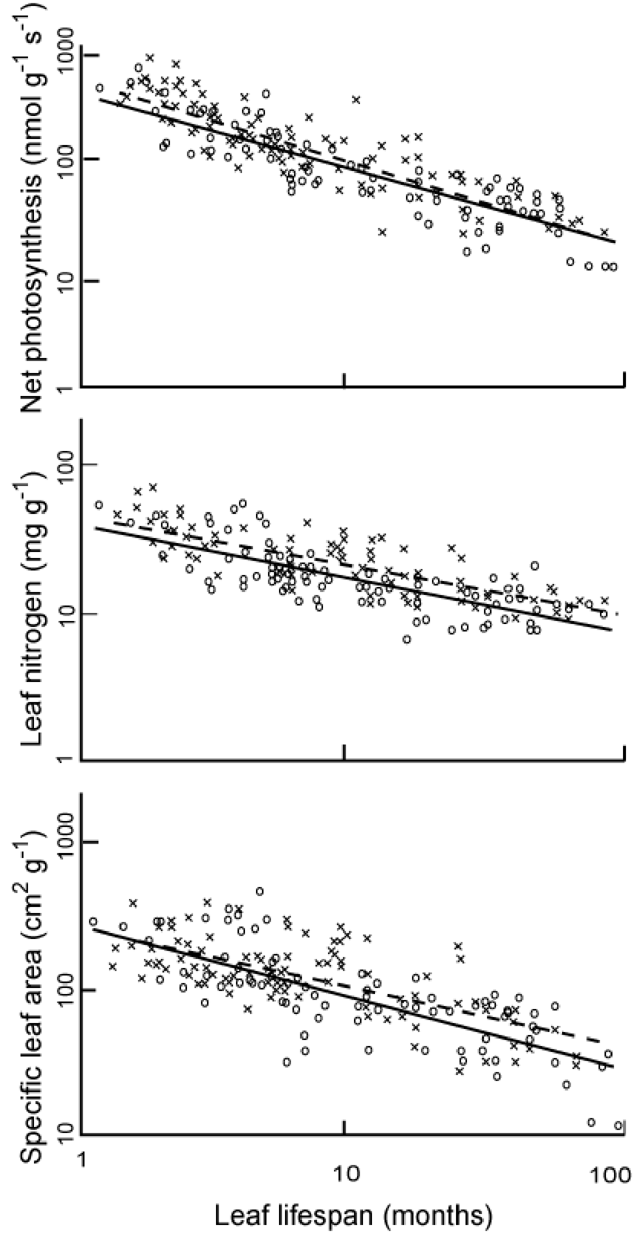
Carbon Input to Ecosystems

•Plants with high photosynthetic rates necessarily have high stomatal conductance (g_s)



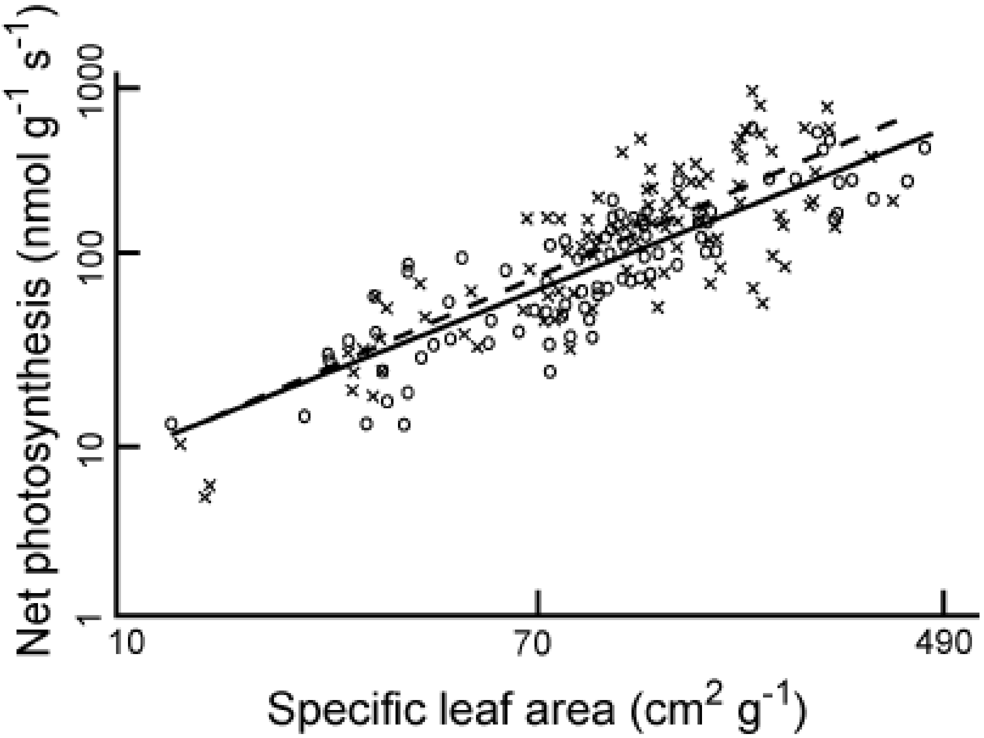
Carbon Input to Ecosystems

- Tradeoff between traits maximizing photosynthesis & leaf longevity
  - In nutrient-limited environments, insufficient nutrients to support rapid leaf turnover
    - Long-lived leaves have ↓ N content, so must photosynthesize longer to “break even”
  - Long-lived leaves contain lots of non-photosynthetic compounds
    - Herbivore protection
    - Desiccation resistant
  - Structural requirements cause long-lived leaves to be dense
    - Surface area per unit biomass, or Specific Leaf Area (SLA; $cm^2\ g^{-1}$)



Carbon Input to Ecosystems

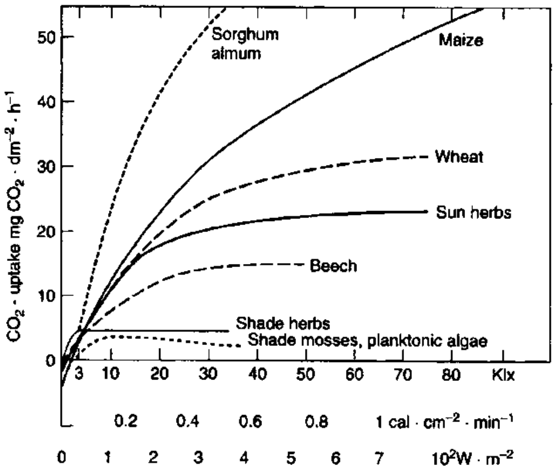
- SLA = surface area / mass (e.g., $cm^2\ g^{-1}$)
  - Good predictor of photosynthetic capacity
    - Easily measured
    - Often used in ecosystem comparisons as an index of photosynthetic capacity



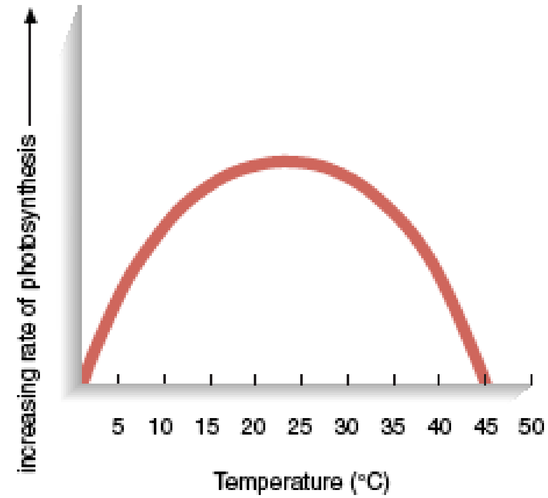
Carbon Input to Ecosystems

- Leaf-level controls over photosynthesis

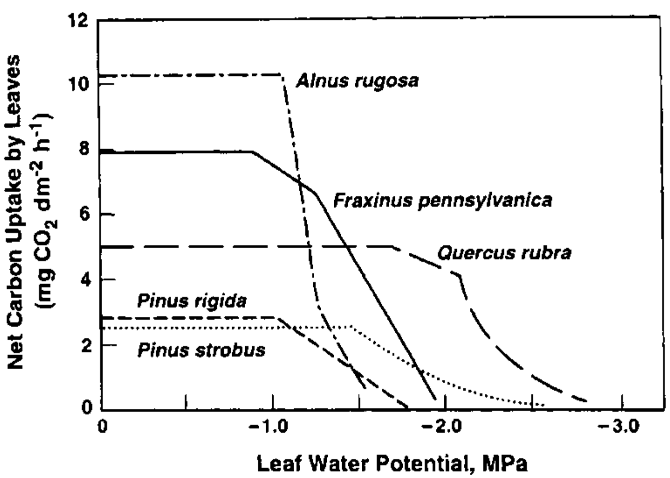
Light



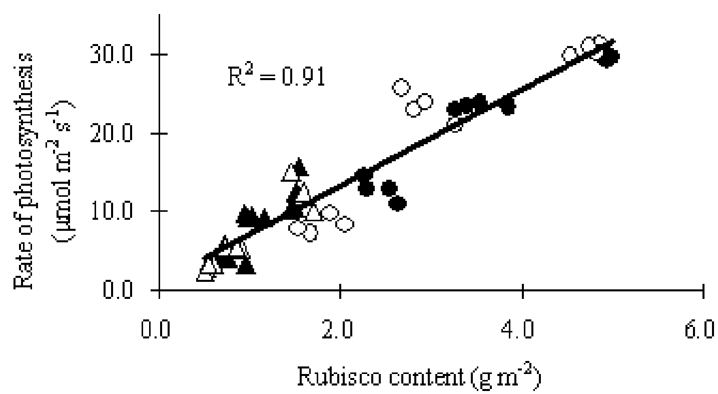
Temperature



H_2O



Nutrients



Carbon Input to Ecosystems

- Suite of physiological traits that influence carbon gain (low vs. high resource env.)
  - Leaf nitrogen concentration
  - Leaf longevity
  - Specific leaf area
  - Growth rate
- All depend to a high degree on availability of soil resources

Carbon Input to Ecosystems

- H_2O limitation reduces the capacity of leaves to match CO_2 supply with light availability
  - Short-term response: reduce stomatal conductance
    - CO_2 supply, *A*, and LUE decline
  - Long-term response: reduce leaf area and/or radiation absorption (reflectance, leaf angle)
    - Increases LUE

Carbon Input to Ecosystems

- WUE = Carbon gain per unit water loss
  - As stomata close, H_2O loss declines to a greater extent than CO_2 absorption
- WUE is high in plants from dry environments
  - WUE is highest in CAM and C4 plants
  - Varies within a given species/individual, seasonally, annually, etc.

Carbon Input to Ecosystems

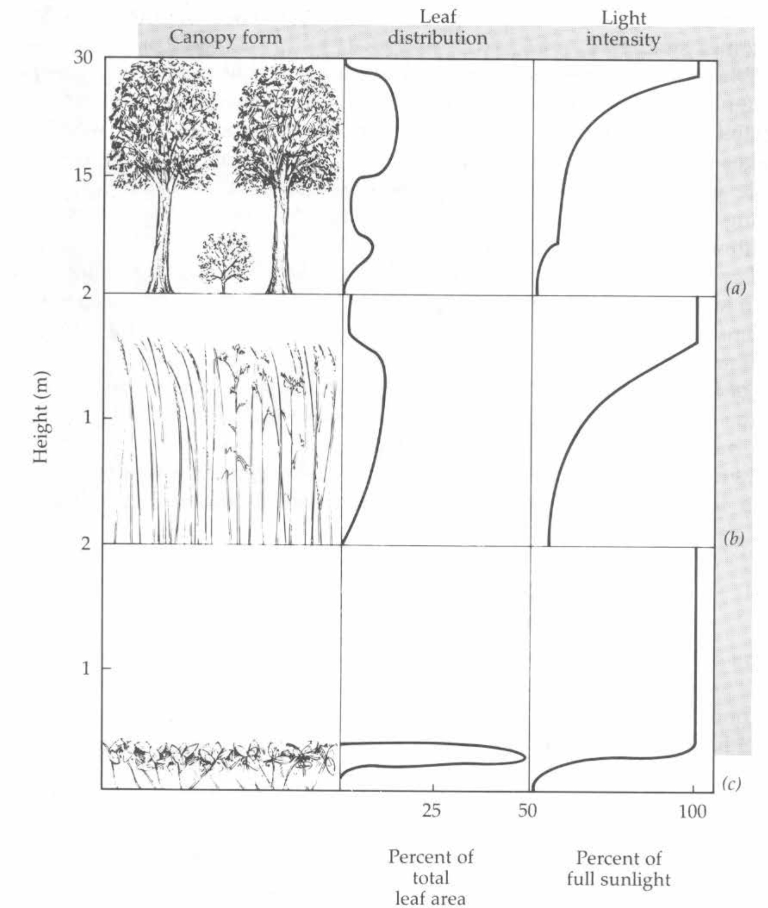
- Canopy controls over GPP
  - Most leaf-level controls still function in entire canopies
  - Leaves at top of canopy carry out most of the photosynthesis
    - Receive most light
    - Typically youngest; most N-rich leaves; high SLA; etc.

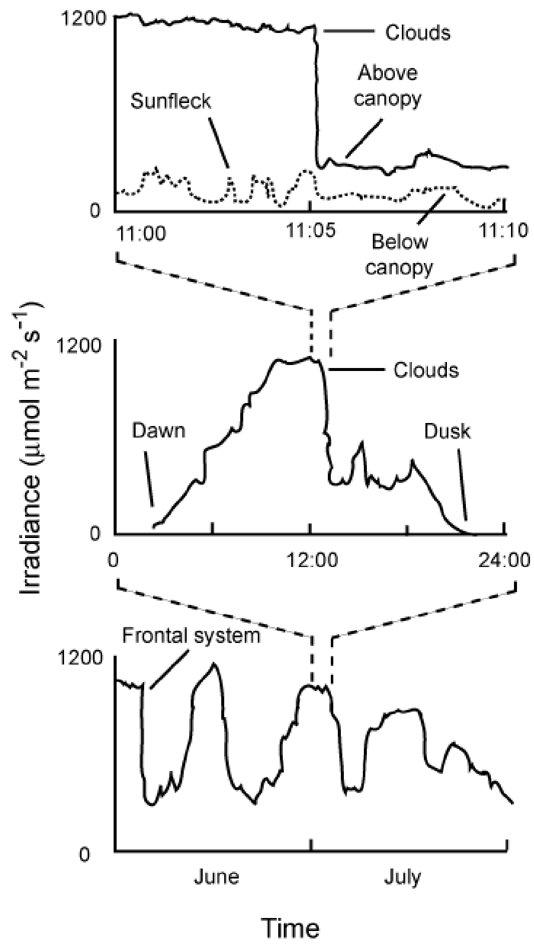
Carbon Input to Ecosystems

- Canopy controls over GPP dominated by:
  - Leaf area
    - often expressed as LAI (leaf area per unit ground area; $m^2\ m^{-2}$)
    - Largely controlled by soil resource availability
  - Growing season length
  - Environmental controls over photosynthesis
    - Important, but secondary, for controlling GPP
    - Most important for controlling Leaf Area

Carbon Input to Ecosystems

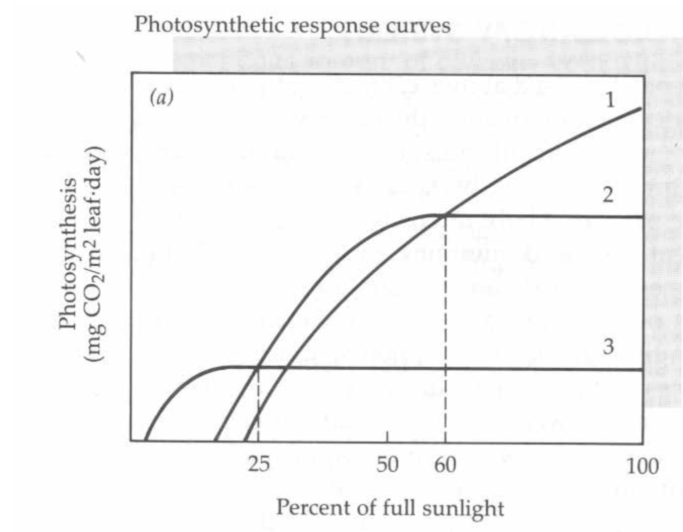
- Canopy controls over GPP
  - Light attenuation thru canopies (sun vs. shade leaves)

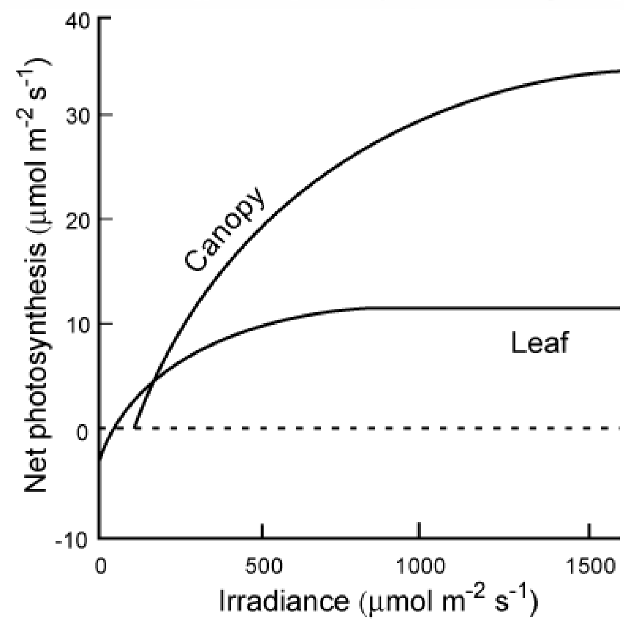




Carbon Input to Ecosystems

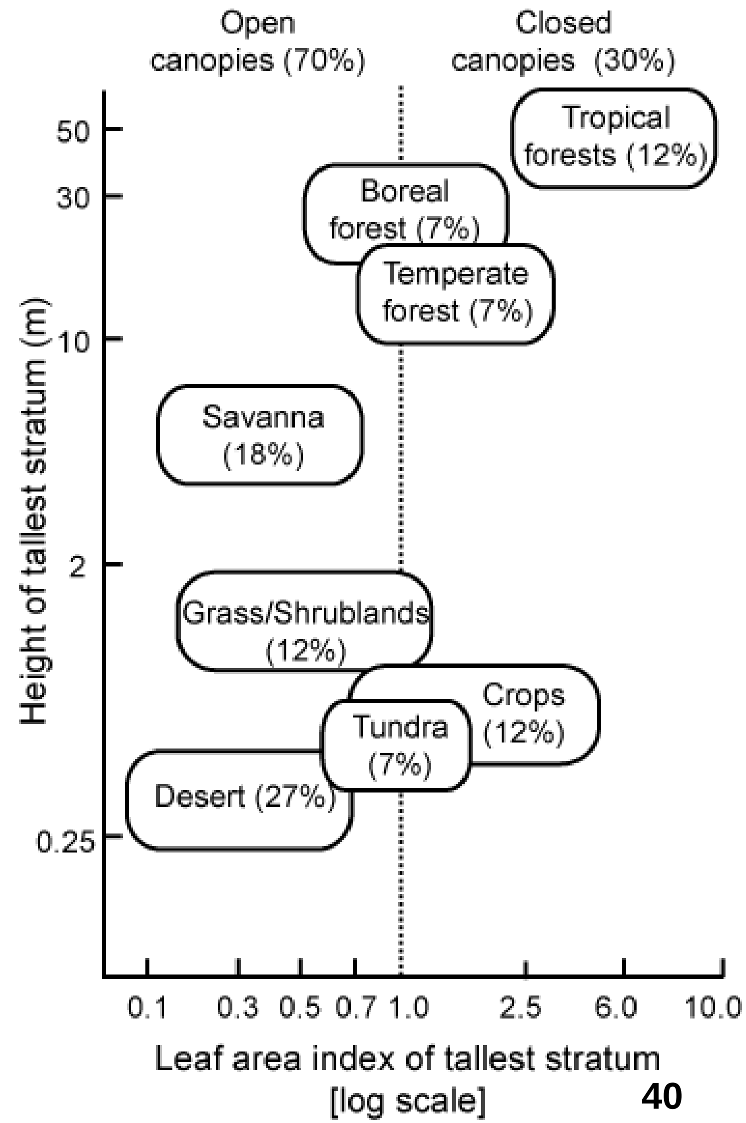
- Canopy controls over GPP
  - Multiple canopy layers maximize C gain potential
  - Light response curve of a canopy maintains constant LUE over a broader range of light availability than a leaf





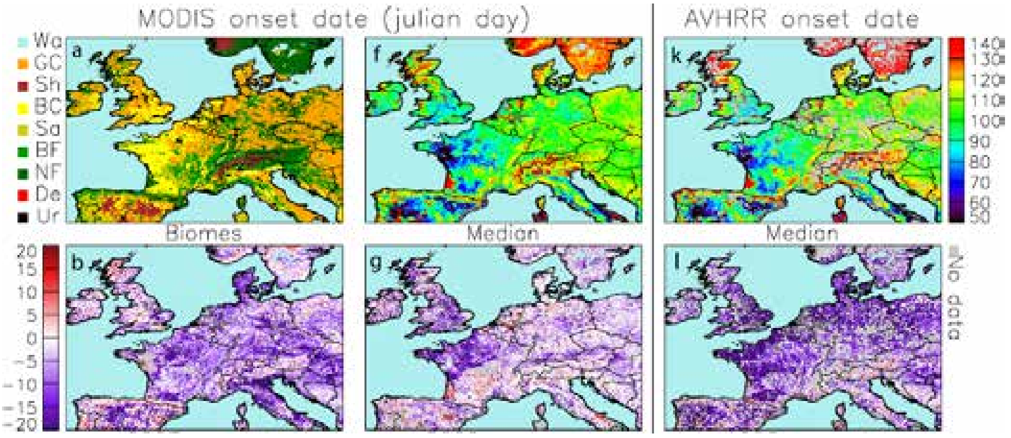
Carbon Input to Ecosystems

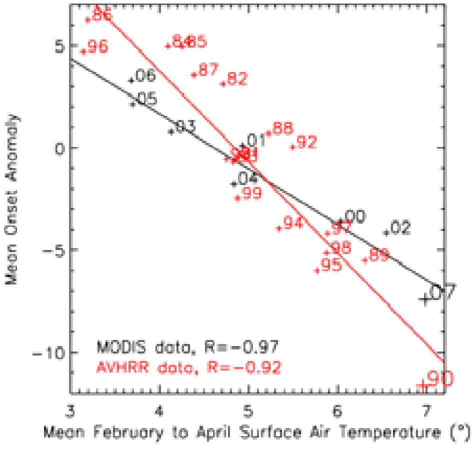
- Most ecosystems have ~open canopies (70% of ice-free area)
- Soil resources largely control LAI
- Close correlation between leaf area and GPP
    - Not so much for really dense canopies



Carbon Input to Ecosystems

- Growing season length response to rising temperatures???
    - Warm winters lead to earlier onset of “greening” and photosynthesis
        - 3.9 days earlier per 1°C rise in winter temp

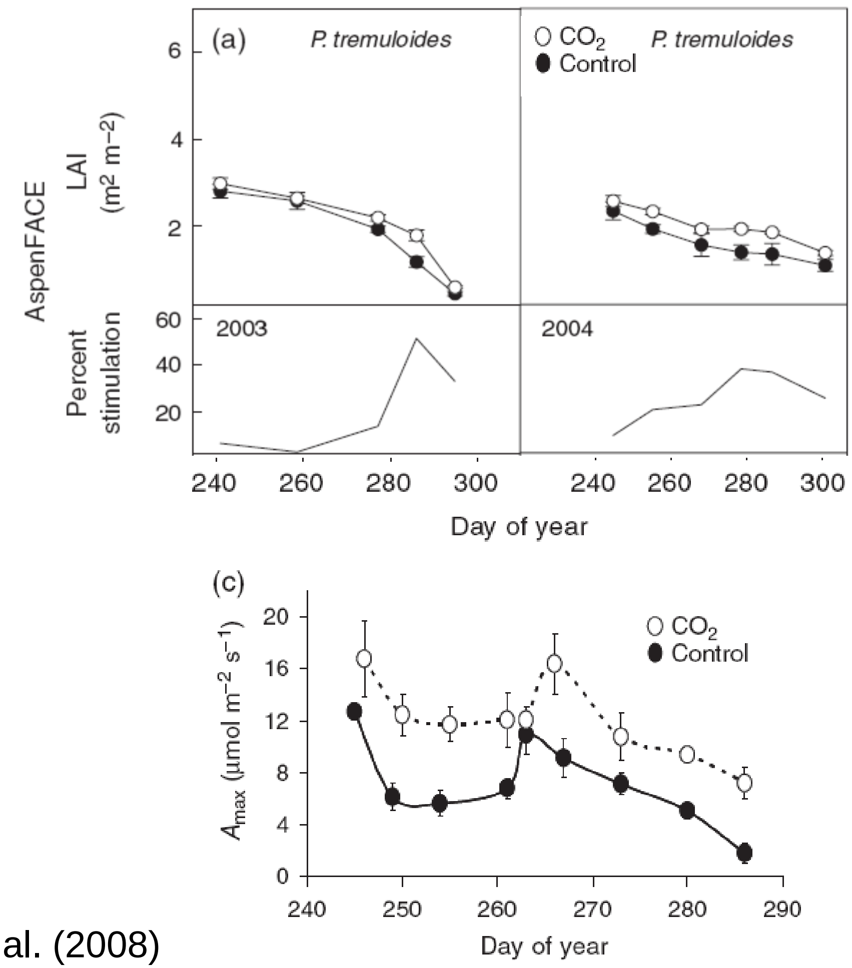




Maignan et al. (2008)

Carbon Input to Ecosystems

- Growing season length increases in response to rising atmospheric CO_2 concentrations
    - Higher CO_2 conc. leads to:
        - Delayed autumnal senescence
        - Increased photosynthetic activity in the fall



Taylor et al. (2008)

Carbon Input to Ecosystems

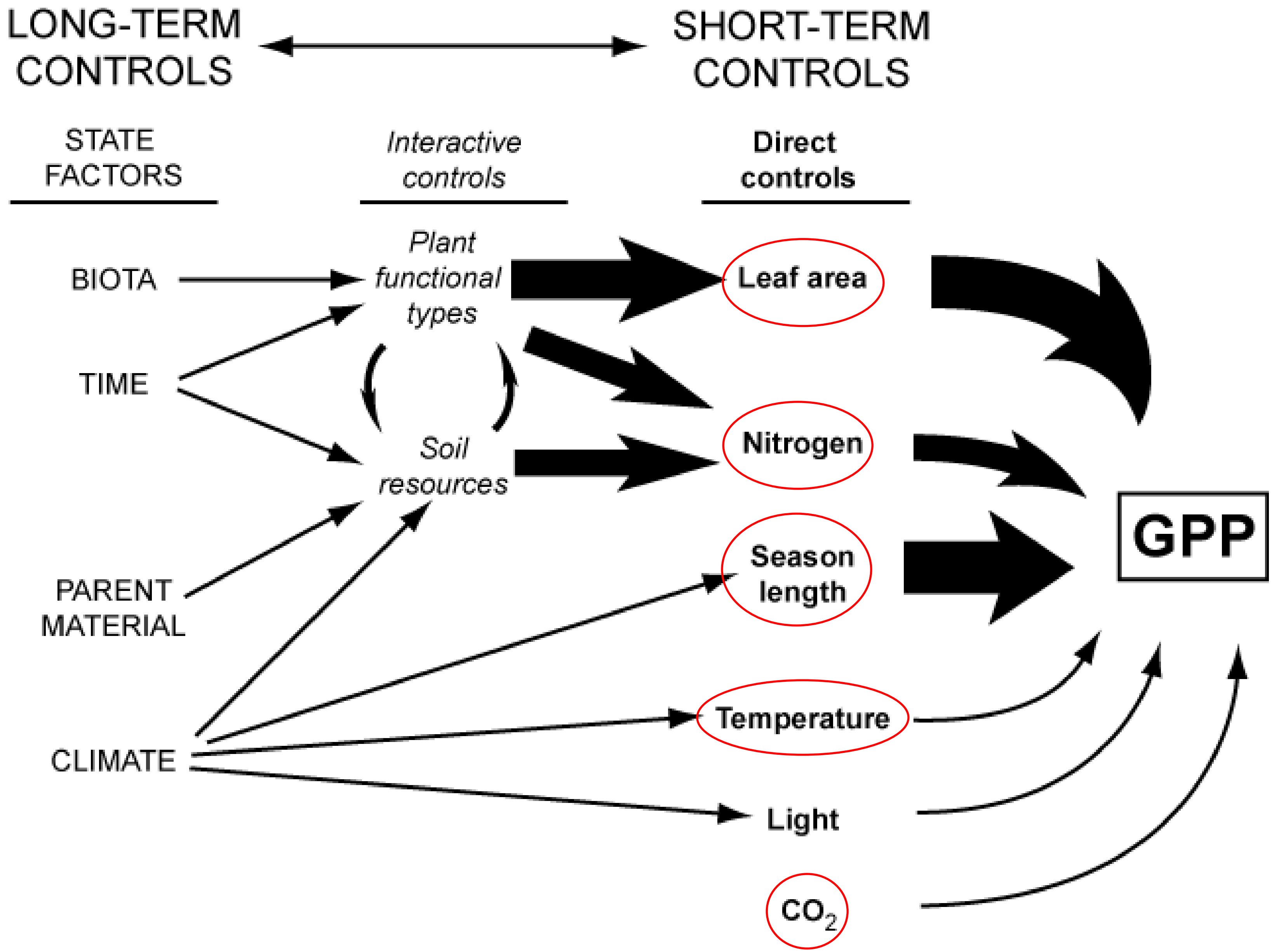
- Take-home points about photosynthesis:

1. <u>Plants balance biochemical and physical limitations to photosynthesis</u>
2. Plants balance photosynthetic capacity with soil resource availability via LAI
3. Plants adjust leaf area to maintain ~constant LUE

Carbon Input to Ecosystems

- Major controls over GPP (net photosynthesis)

1. Quantity of leaf area
   - Reduced by herbivores and pathogens
2. Length of photosynthetic season
   - Global climate change?
3. Photosynthetic rate of individual leaves
   - Inherent photosynthetic capacity
   - Environmental stress



Which are being altered by humans?

Carbon Input to Ecosystems

- How do you measure GPP?
  - Measure photosynthesis of every leaf in the canopy?

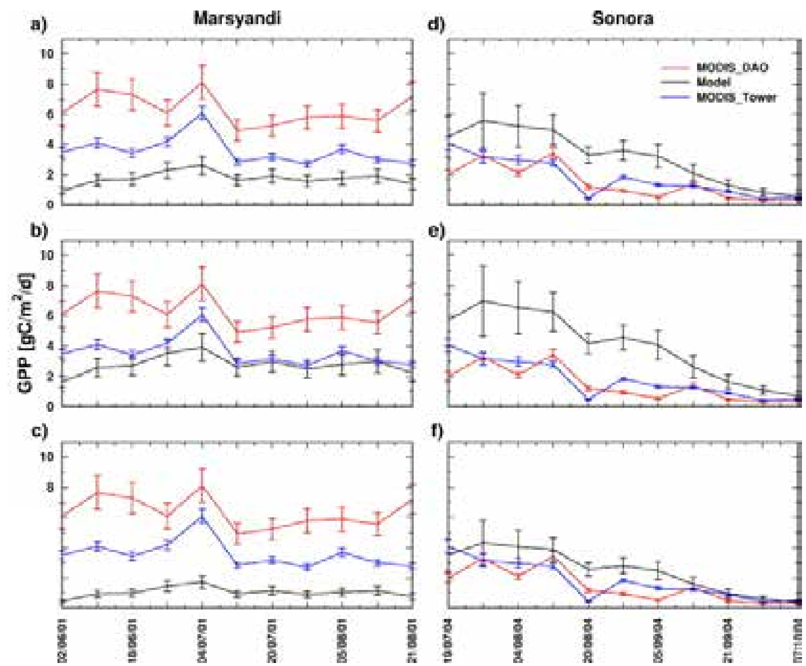
→

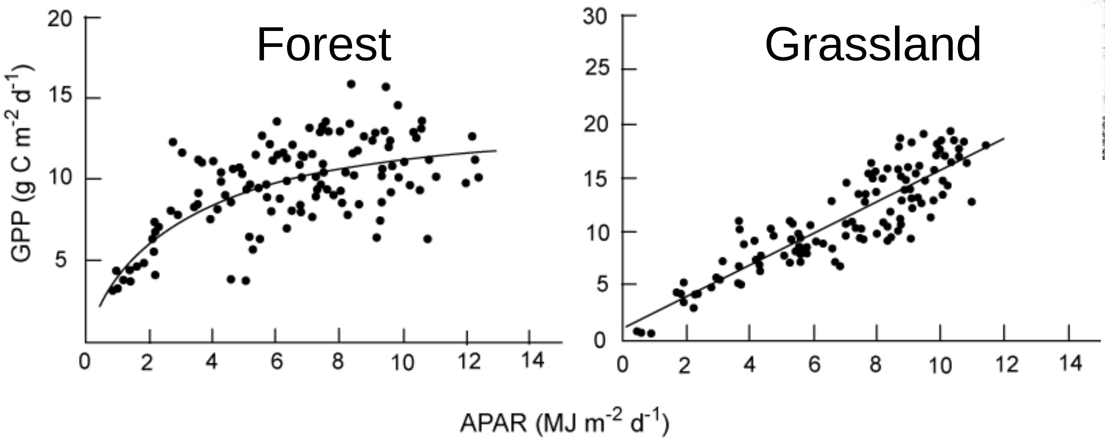
→

  - Measure a few leaves and scale to the canopy?

Carbon Input to Ecosystems

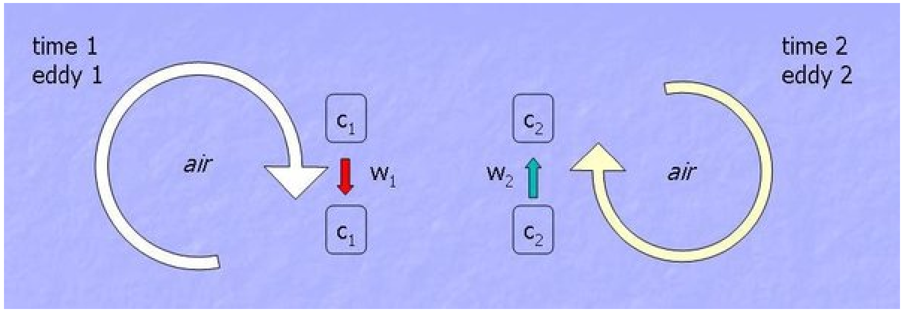
- How do you measure GPP?
  - RS / Modeling studies
    - LAI estimates from remote sensing (and/or field studies)
    - APAR from remote sensing
    - LUE from existing studies
    - Plug it all into a TEMs or DGVM





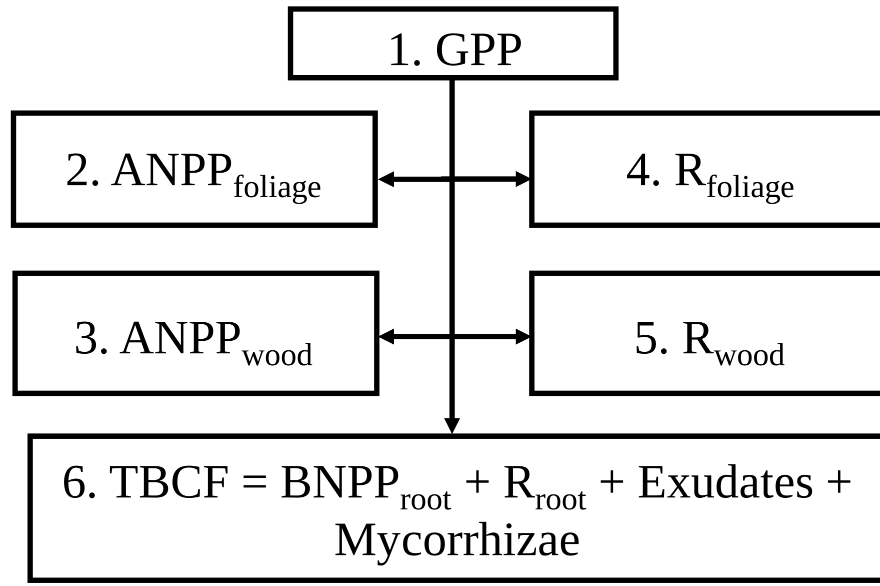
Carbon Input to Ecosystems

- How do you measure GPP?
  - Eddy flux / covariance
    - CO_2 sensor above the canopy
      - Vertical flux of CO_2 is a function of the covariance of wind velocity and gas concentration
    - Really measure Net Ecosystem Exchange (NEE)
      - NEE = GPP - $R_{ecosystem}$



Carbon Input to Ecosystems

- How do you measure GPP?
  - Sum of individual components
    - Need measurements of all the individual components
    - Only ~30 studies worldwide



Litton et al. (2007)