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for Climate Research

CHESS land surface modeling course

Controls of Carbon Input to Terrestrial Ecosystems: photosynthesis

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Outline: carbon input and its main controls

- **What is photosynthesis?**
  - Photosynthetic pathways (C_3, C_4, CAM)
- What is Gross Primary Production (GPP)?
  - Leaf scale -> canopy scale -> ecosystem scale
- What are the controls of photosynthesis and GPP?

Leaf scale
Light limitation
CO2 limitation
Nitrogen limitation
Leaf traits & photosynthetic capacity
Water limitation
Other effects

Ecosystem scale
Controls on leaf scale
+
Controls on canopy scale:
Leaf area
Photosynthetic season

What is photosynthesis?

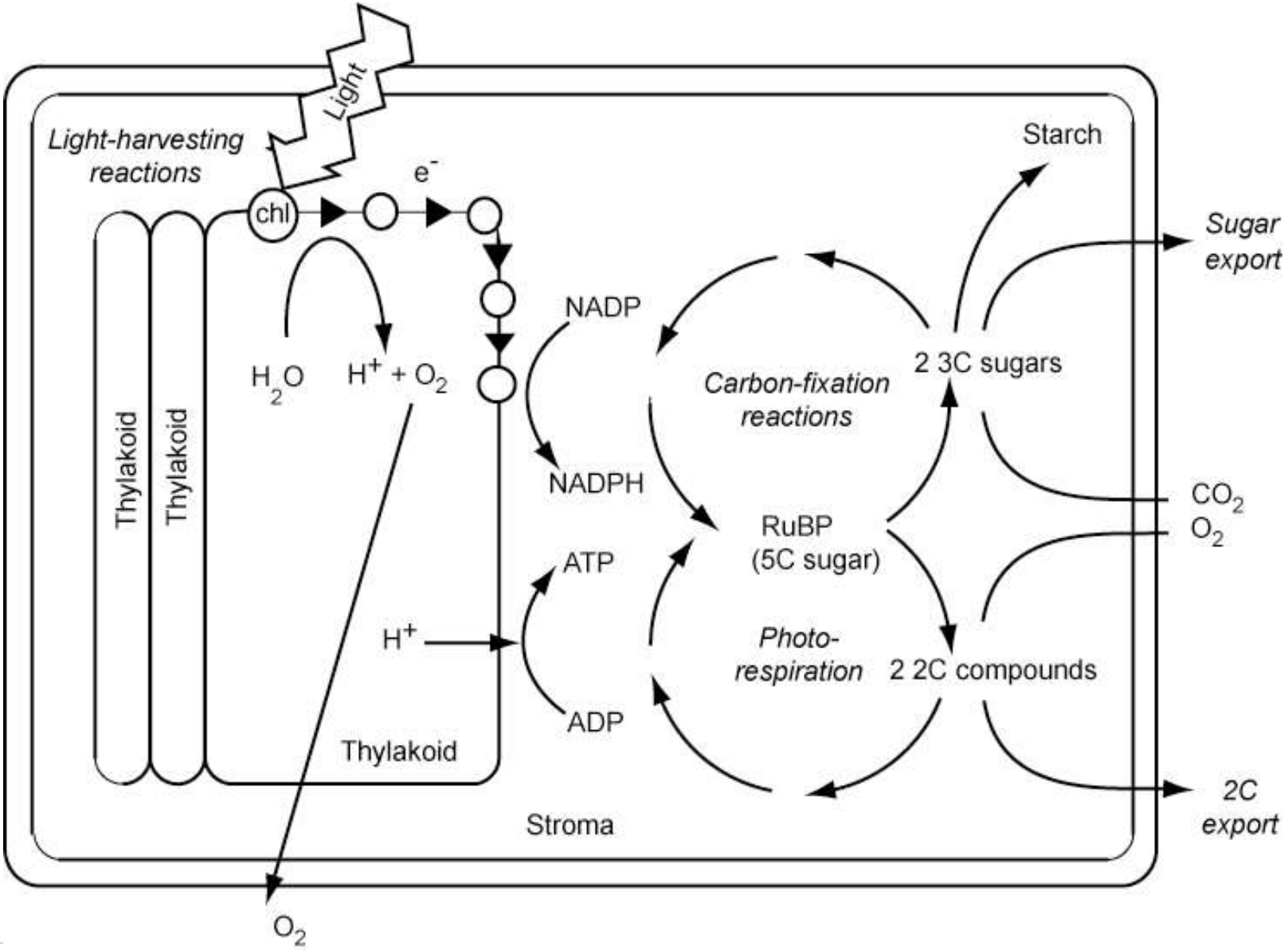
Transforming energy & materials

› **light-harvesting reactions** (solar to chemical energy)

-> **chlorophyll**

› **carbon-fixation reactions** (CO_2 into sugars)

-> **Rubisco**

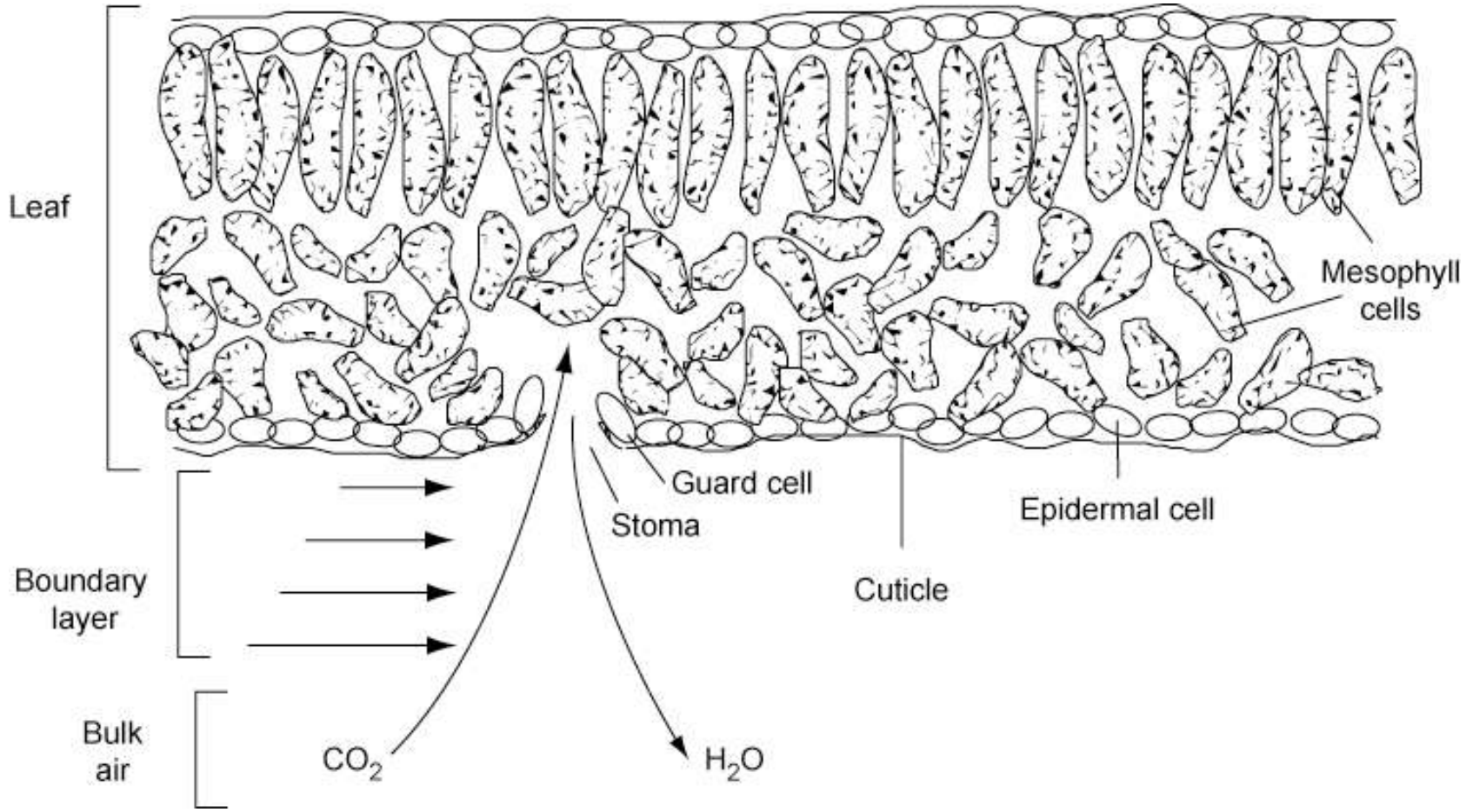


Chapin et al., 2011

What is photosynthesis?

Key definitions

- **Net photosynthesis** (C fixation – respiration)
- **Boundary layer**
- **Stomata**
- **Transpiration**
- **Stomatal conductance**

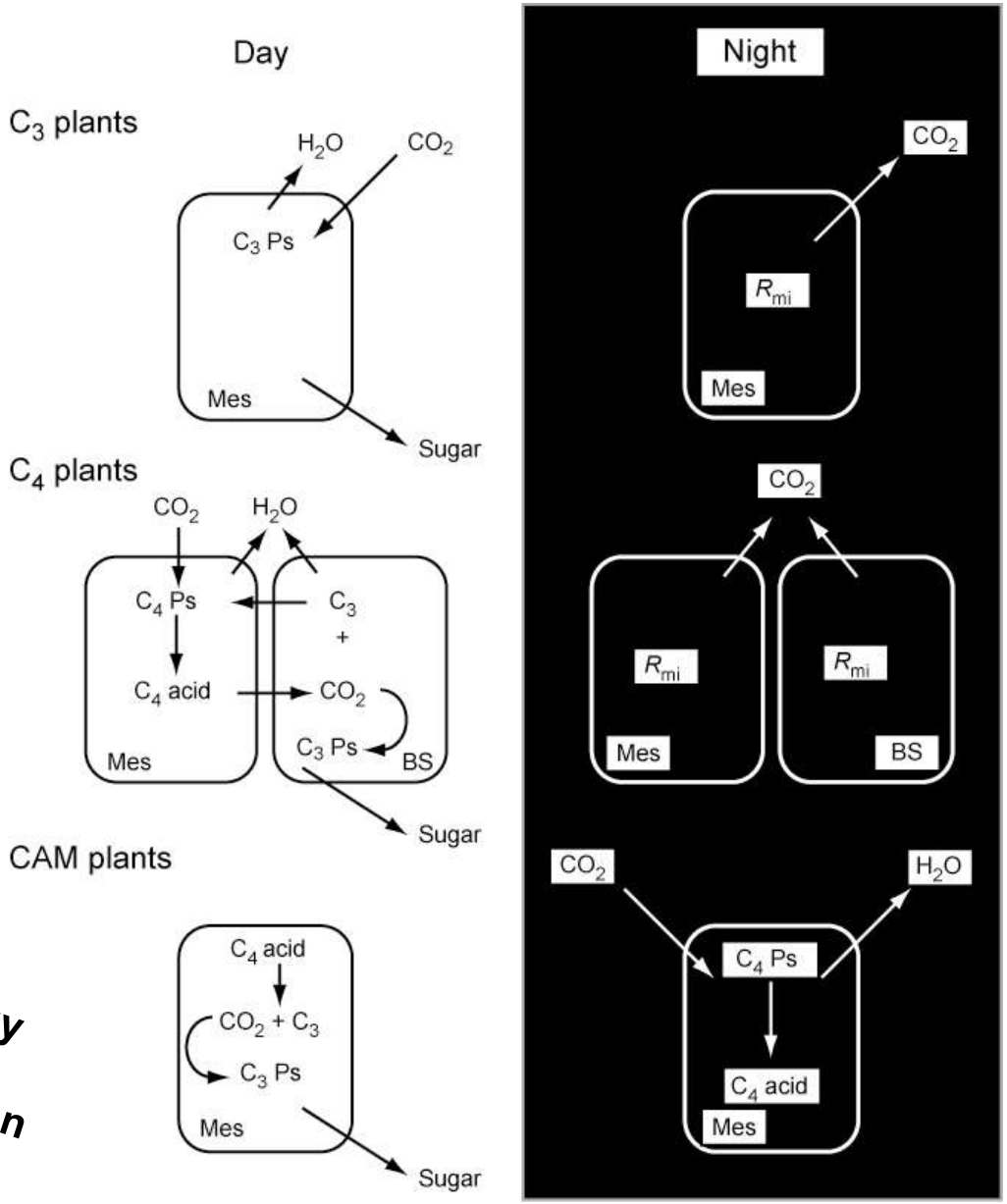


Chapin et al., 2011

Different pathways, same objective

Transforming energy:
Light energy to chemical energy

Transforming materials: C fixation



Chapin et al., 2011

What is photosynthesis?

C_4 vs. C_3

- Advantage: higher efficiency of Rubisco
  - -> Less nitrogen requirement
  - -> Less water loss
  - -> Isotopic signature (^{13}C)
- Disadvantage: higher energy cost per C fixed
  - -> requires: high temperature &
  - -> high light conditions (e.g. tropical)

Carbon input and its main controls

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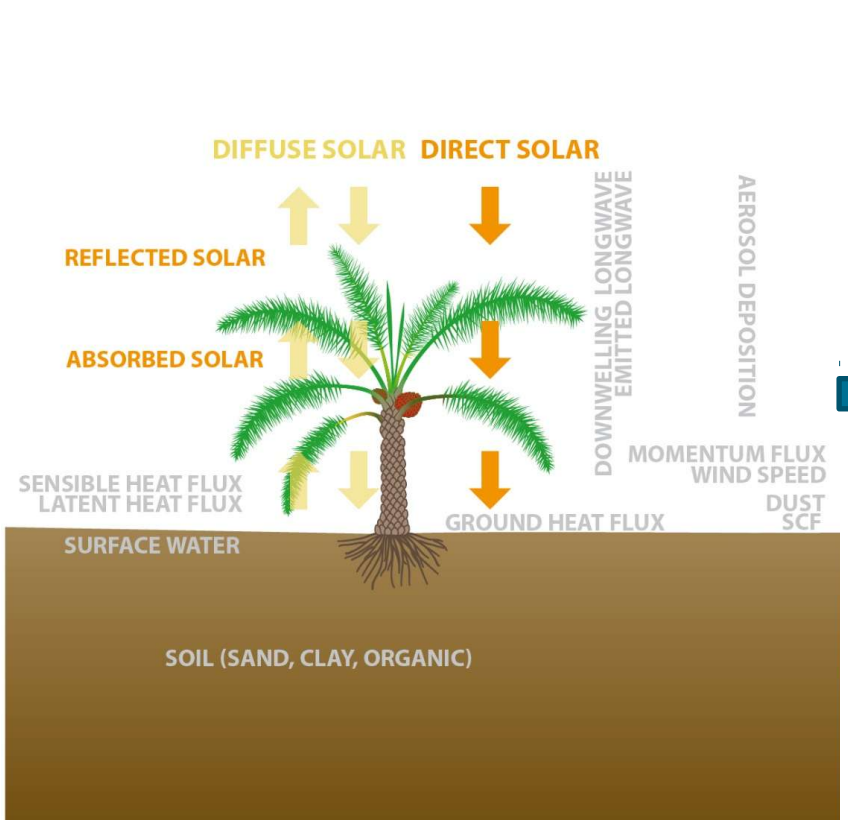
What is Gross Primary Production?

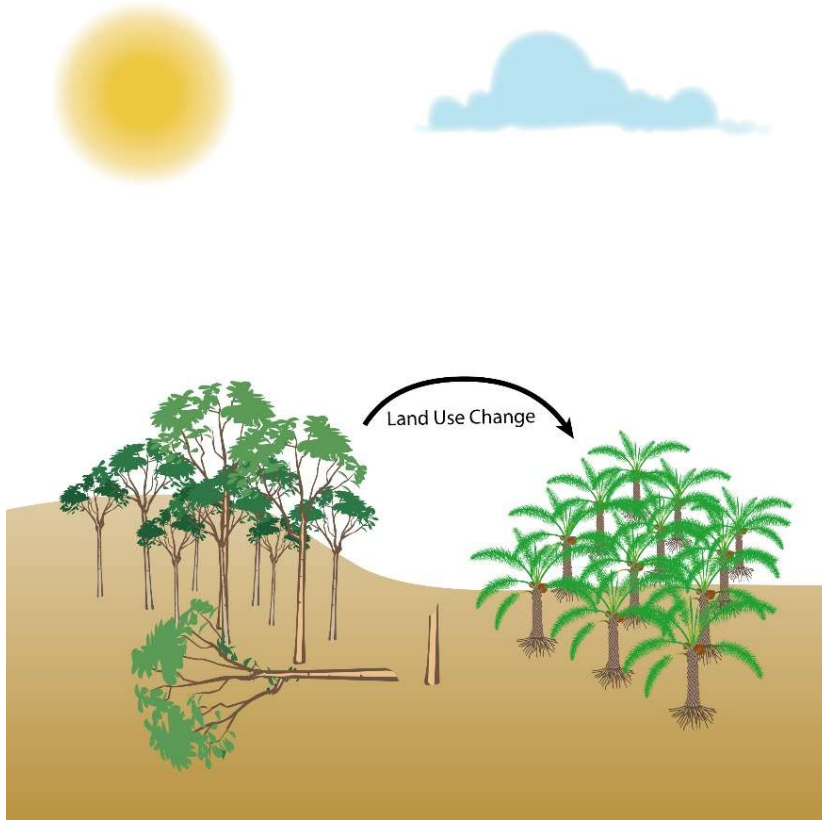
Gross Primary Production (GPP) is the sum of the net photosynthesis by all photosynthetic tissue (e.g. leaves) measured at the ecosystem scale

Leaf scale -> canopy scale -> ecosystem scale

GPP of terrestrial ecosystems integrates the effects of environmental factors and leaf photosynthetic properties through the canopy

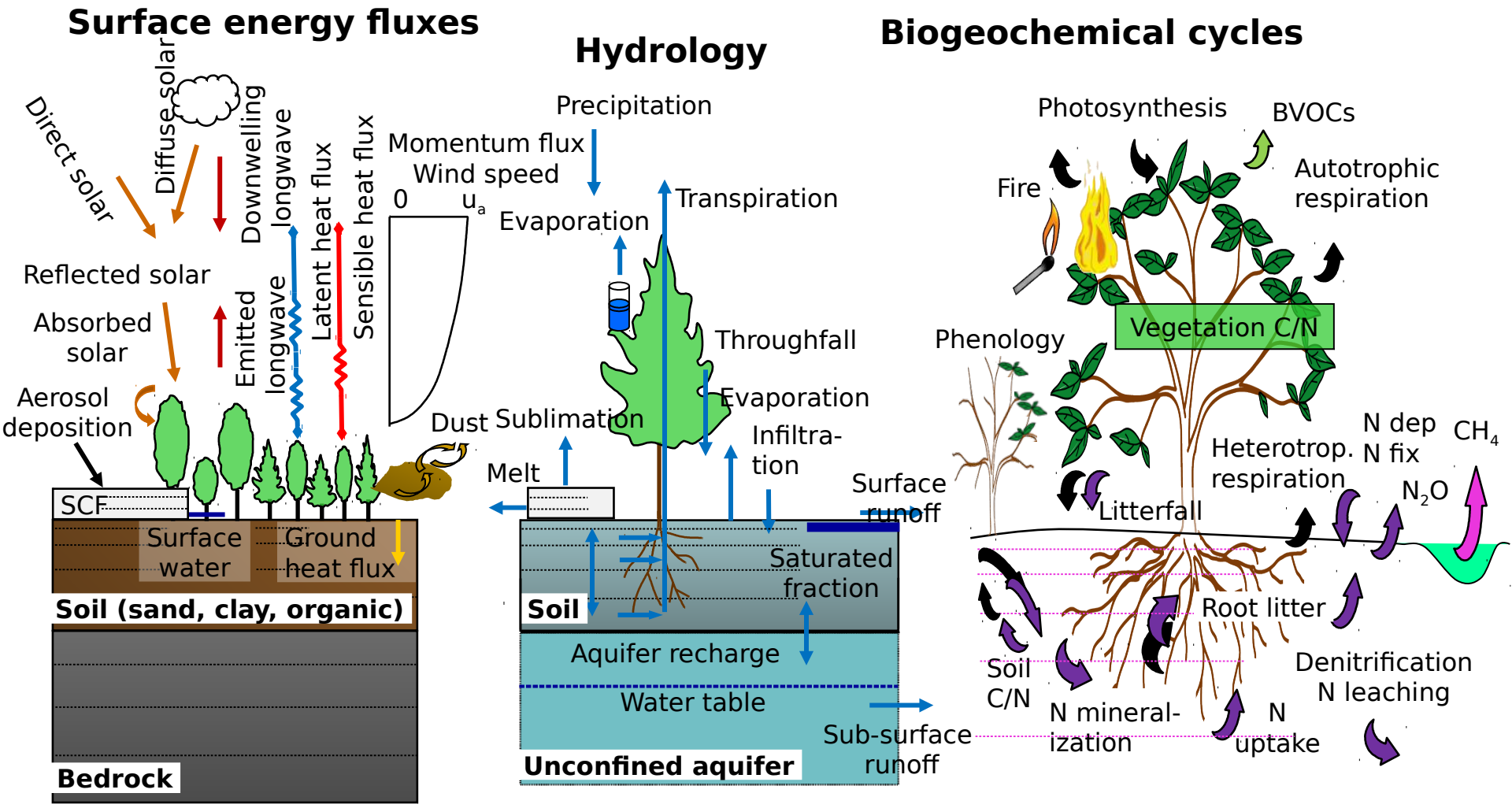
Scaling up from leaf to canopy to ecosystem





Fan et al., 2016

Community Land Model (CLM4.5)



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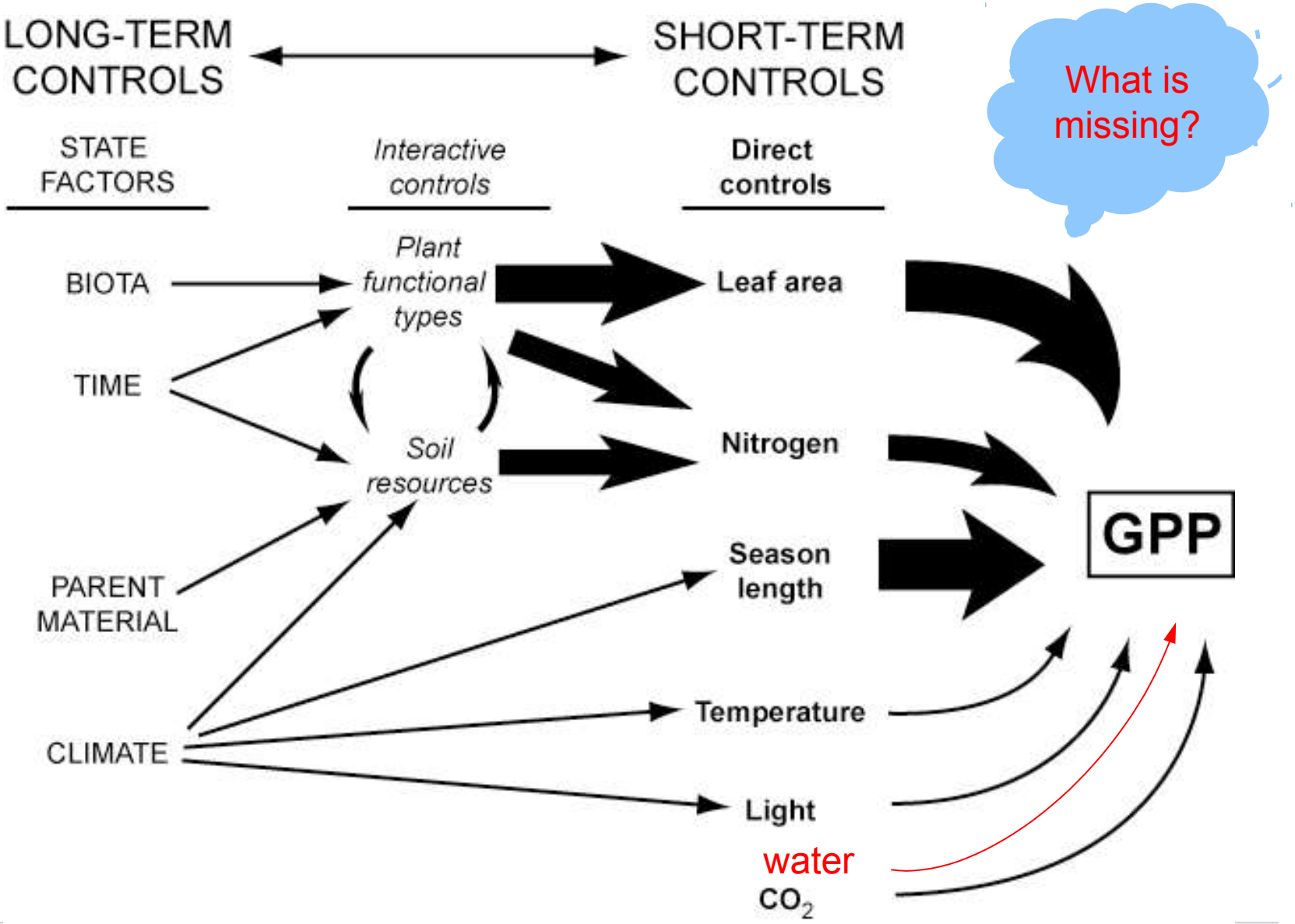
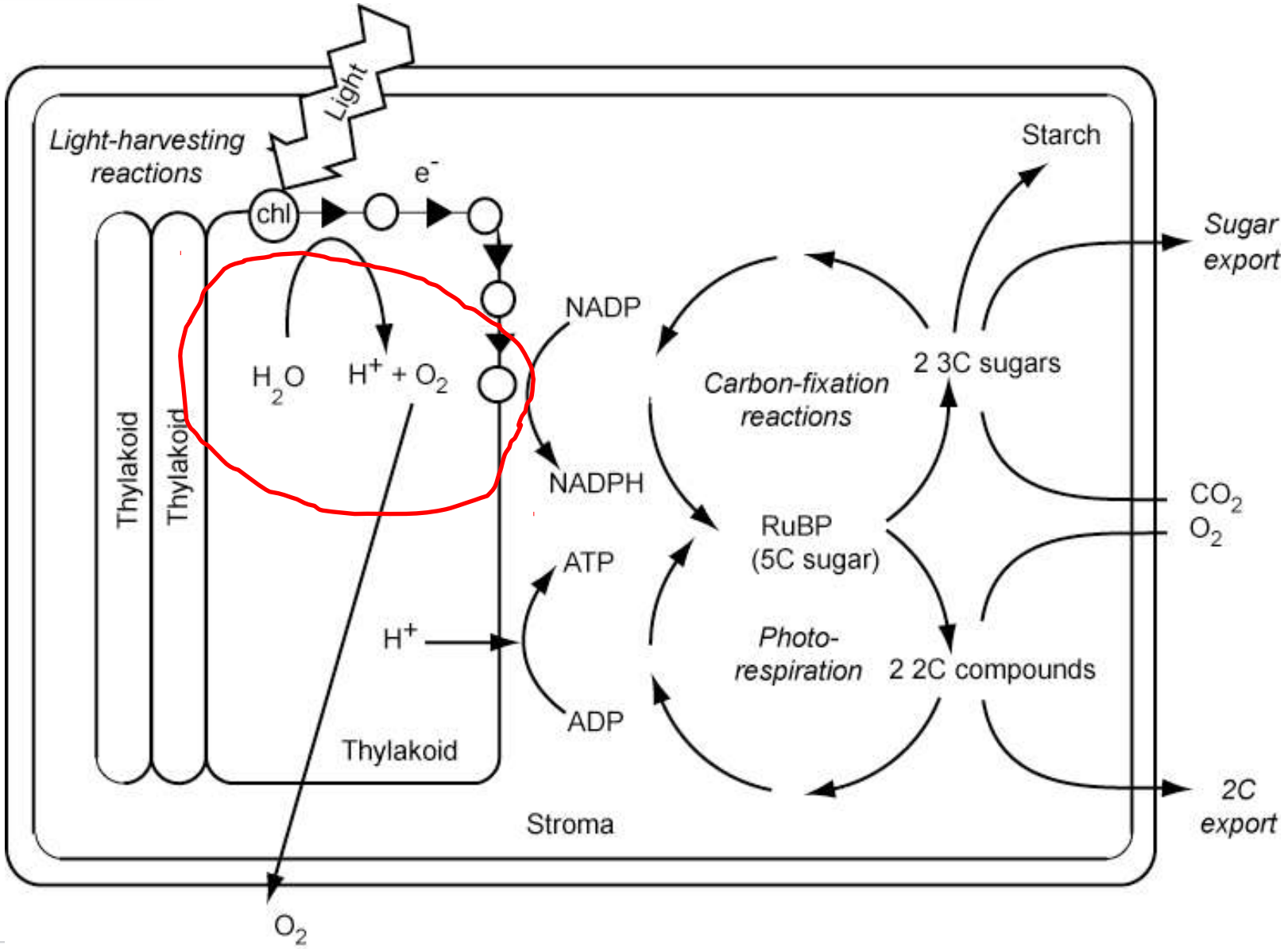


Chapin et al., 2011

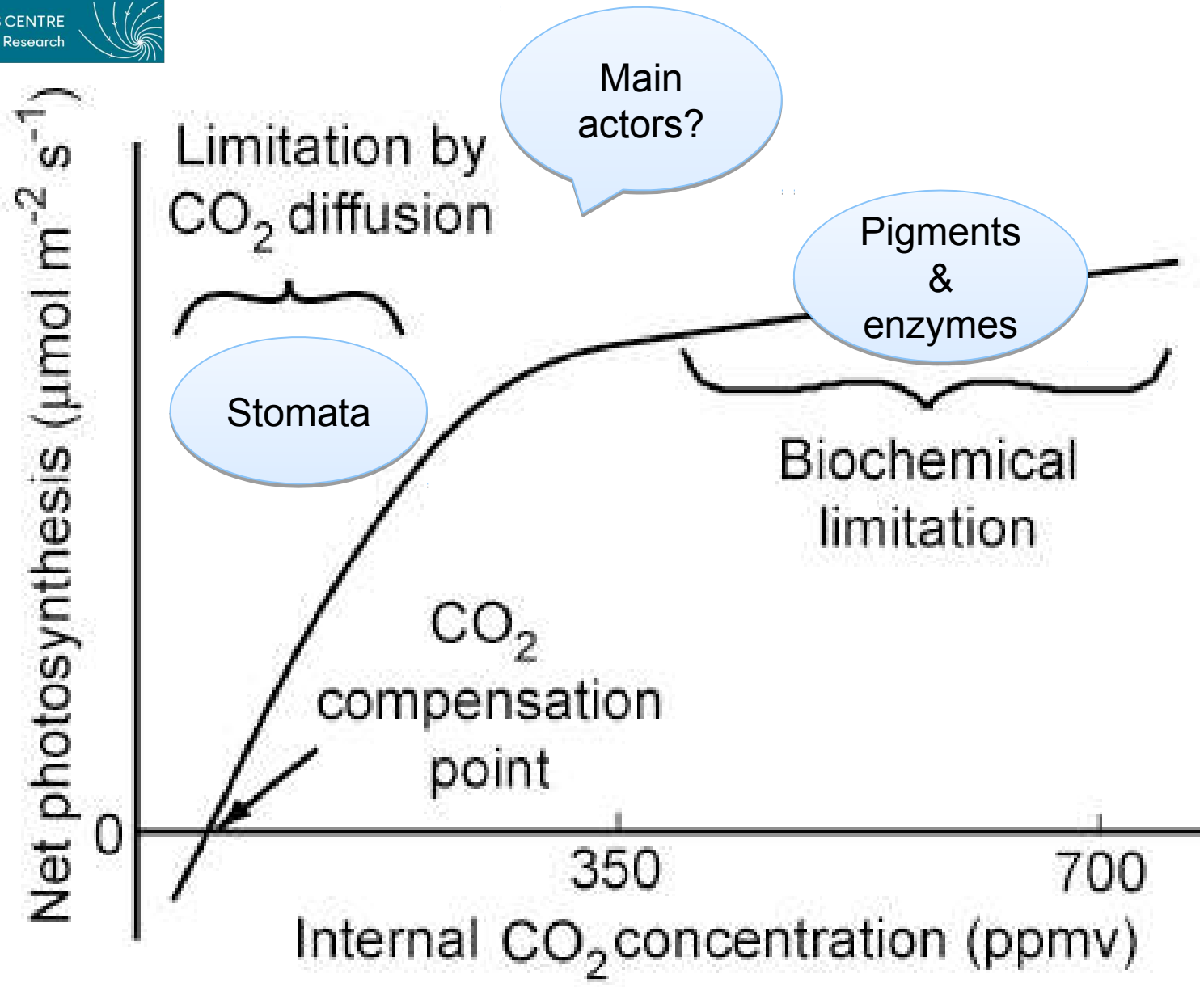


Chapin et al., 2011

What are the controls of carbon input?

	Leaf scale	*Basic principle*
biophysical?	Leaf traits & photosynthetic capacity	**CO_2 diffusion** (stomata) matches **biochemical capacity** (Rubisco)
environmental?	CO2 limitation Light limitation Nitrogen limitation Water limitation Other effects	Co-limitation on C fixation

Review Question 1. How do light, CO2 , and nitrogen interact to influence the biochemistry of photosynthesis in C3 plants? What biochemical adjustments occur when each of these resources declines in availability?



Chapin et al., 2011

What are the controls of carbon input?

CO_2 limitation

Changes in stomatal conductance by leaves minimize the effects of CO2 supply on photosynthesis.

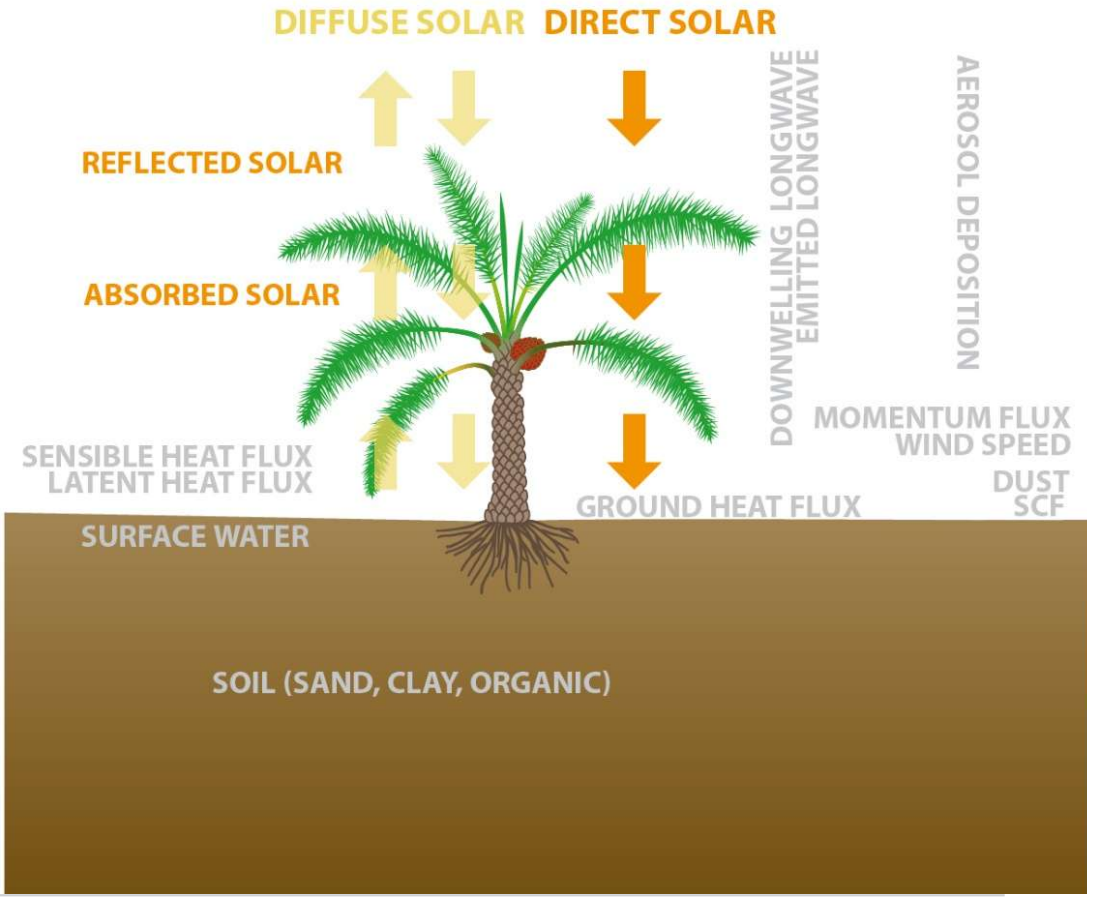
Free atmosphere (little spatial variation and competition)

CO_2 rising & fertilization (substantial temporal variation)

What are the controls of carbon input?

Light limitation

Physical environment determines light inputs to ecosystems, and leaf area governs the distribution of light within the canopy.



Fan et al., 2016

Light extinction function within canopy

- Irradiance decreases from the top of canopy (I_0)

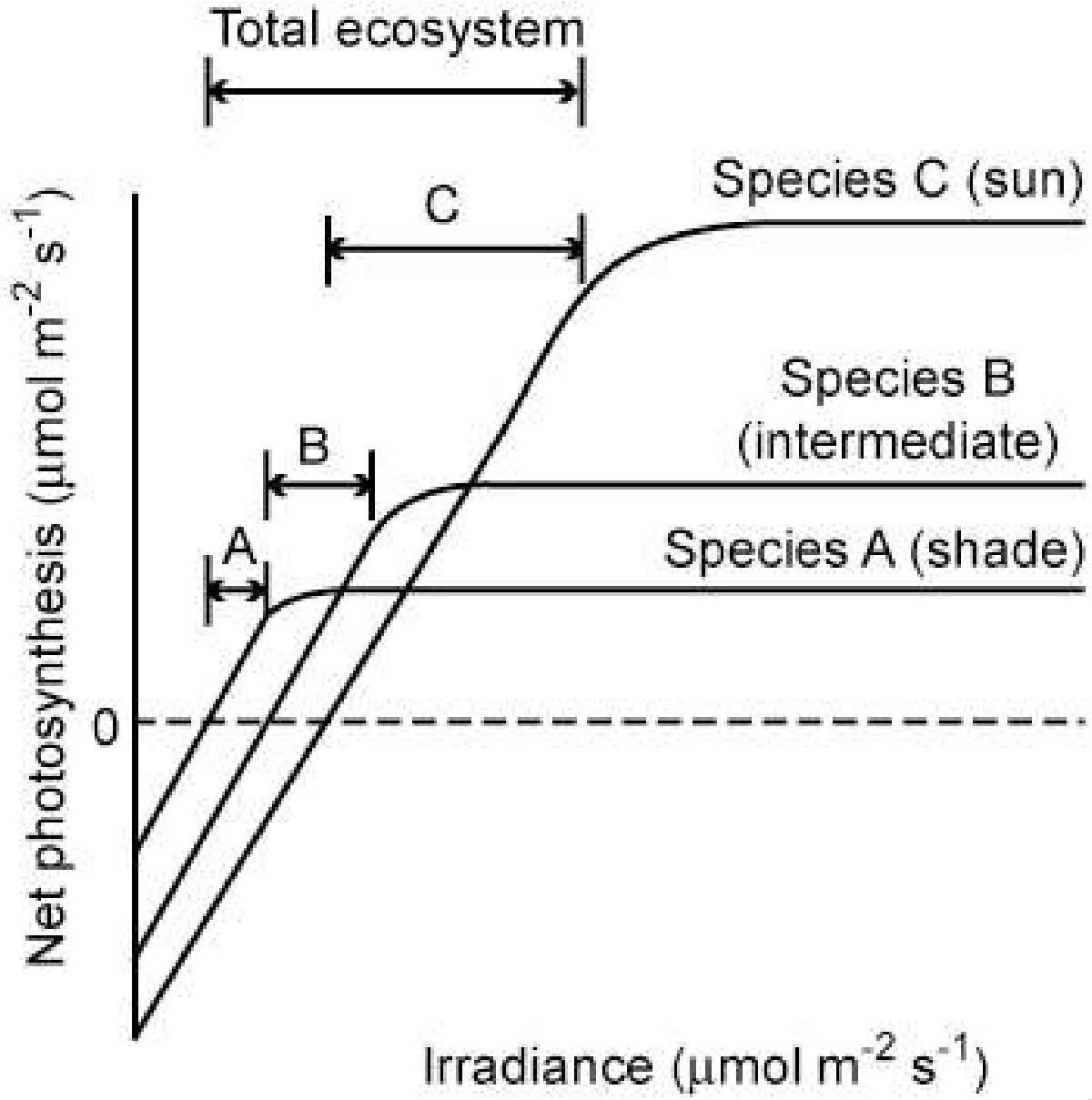
$$I_z = I_0 e^{-K \sum_{z=1}^{n} LAI_z}$$

Controlled by sunlit area of direct solar beam

$$f_{sun}^{z} = e^{-K \sum_{z=1}^{n} LAI_z}$$

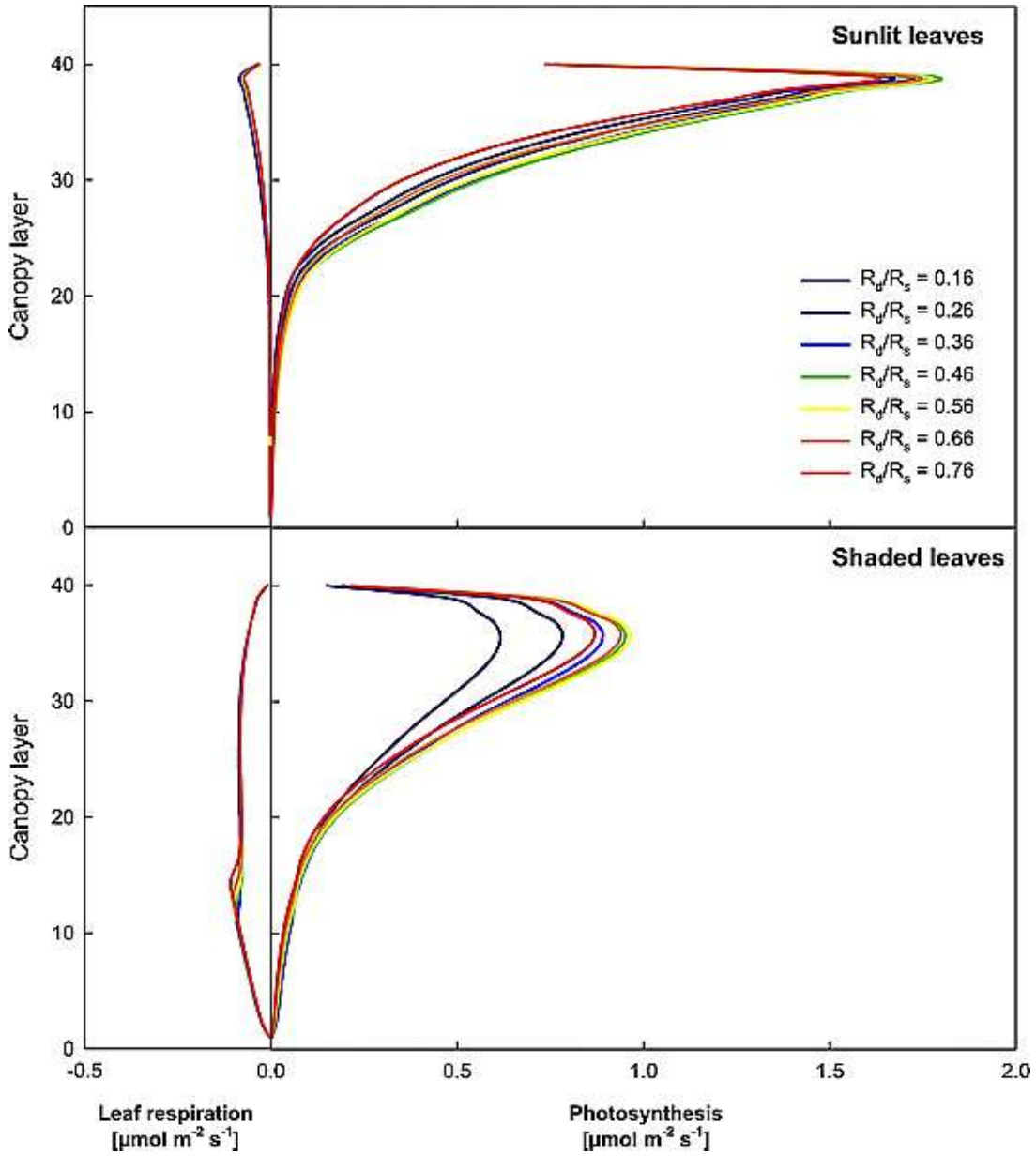
K is extinction coefficient $K(\theta, \emptyset) = \frac{G(\theta,\emptyset)}{cos\theta}$

where the G function (zenith, azimuth) defines the mean relative projected area of vegetative elements (leaf and stem) in the direction of incident radiation



Chapin et al., 2011

Effects of diffuse radiation on canopy gas exchange processes in a forest ecosystem

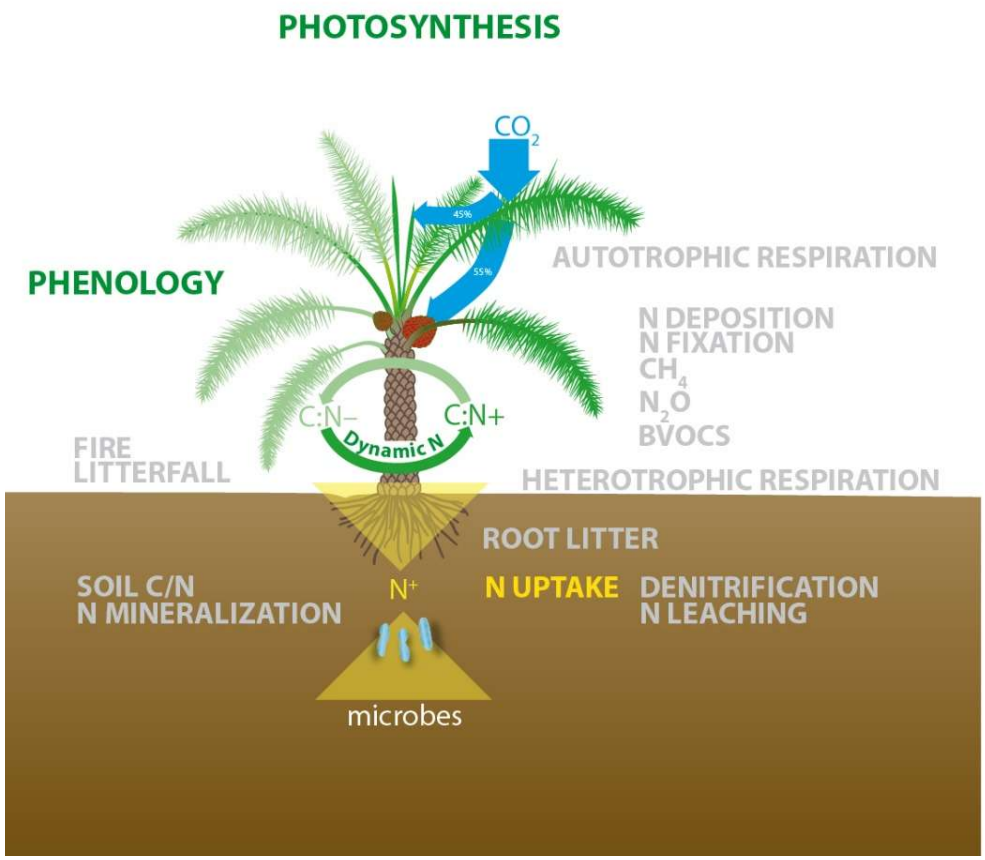


Knohl and Baldocchi. 2008.

What are the controls of carbon input?

Nitrogen limitation

Photosynthetic capacity correlates strongly with leaf nitrogen concentration because photosynthetic enzymes (Rubisco) account for a large proportion of the nitrogen in leaves



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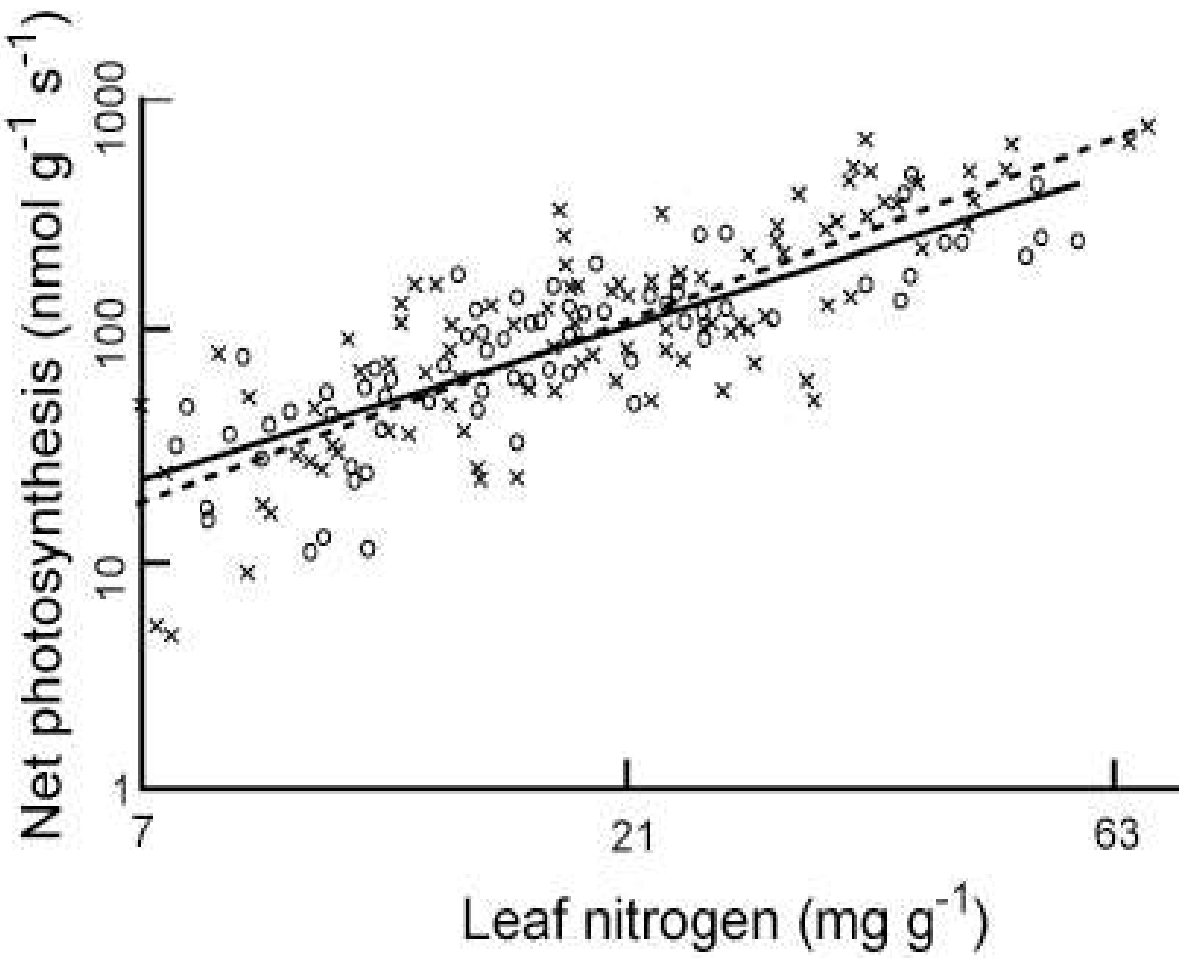


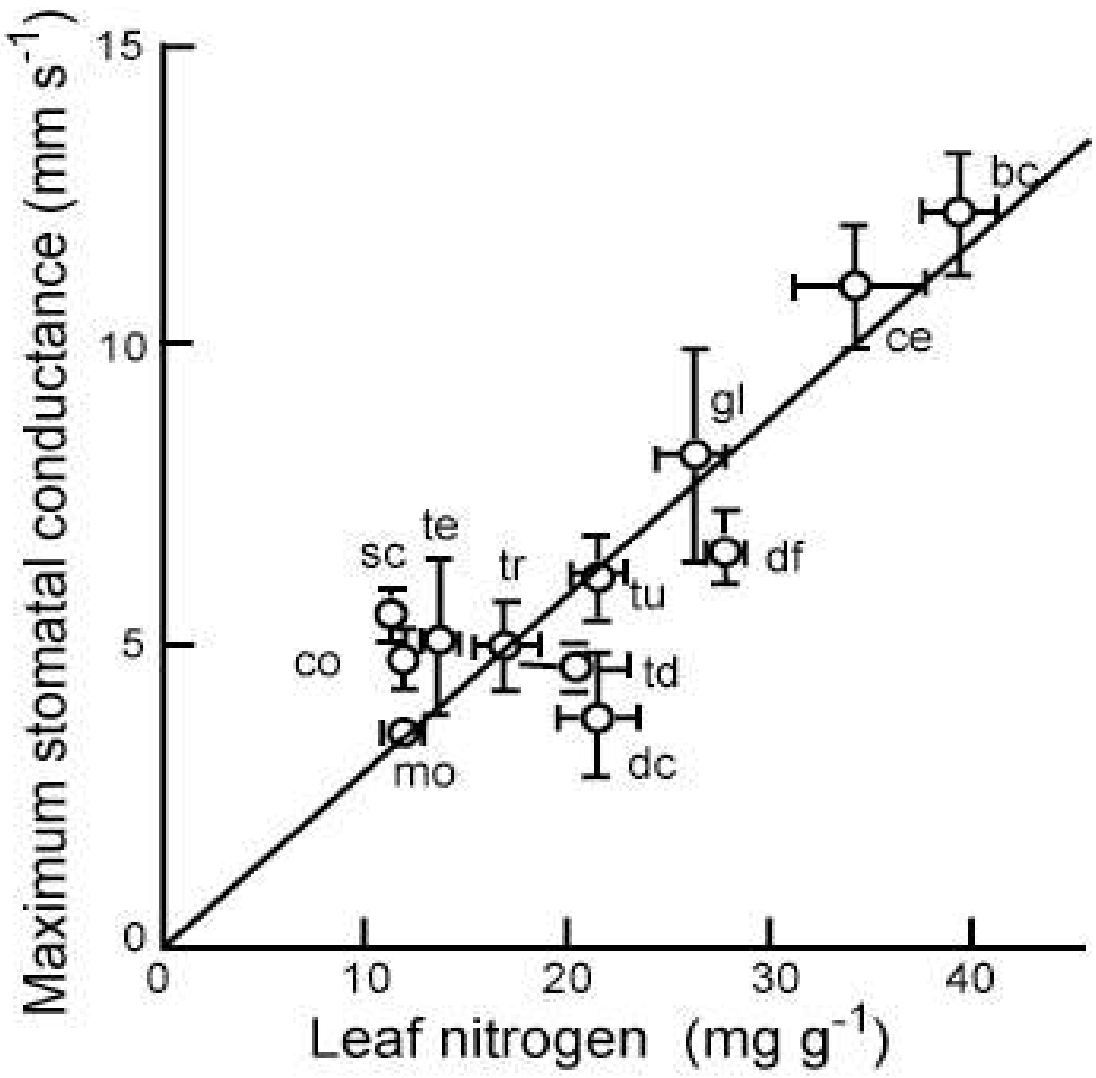
Chapin et al., 2011

Co-limitation on C fixation

CO_2 diffusion (stomata)

≈

Biochemical capacity
(Rubisco)



Chapin et al., 2011

Photosynthetic capacity (area based)

- **Maximum rate of carboxylation** (Rubisco-limited)

$$V^0_{cmax25} = \frac{1}{CN_{leaf} SLA_0} F_{LNR} F_{NR} a_{R25}$$

Leaf scale

Canopy scale

$$V^z_{cmax25} = V^0_{cmax25} \times e^{-K_N \sum_{z=1}^{n} LAI_z}$$

GPP

Photosynthesis in the CLM model

```
! Default
if (vcmax_opt == 0) then
   ! vcmax25 at canopy top, as in CN but using lnc at top of the canopy
   vcmax25top = lnc(p) * flnr(patch%itype(p)) * fnr * act25 * dayl_factor(p)
   if (.not. use_cn) then
      vcmax25top = vcmax25top * fnitr(patch%itype(p))
   else
      if ( CNAllocate_Carbon_only() ) vcmax25top = vcmax25top * fnitr(patch%itype(p))
   end if
else if (vcmax_opt == 3) then
   vcmax25top = ( i_vcad(patch%itype(p)) + s_vcad(patch%itype(p)) * lnc(p) ) * dayl_factor(p)
else if (vcmax_opt == 4) then
   nptreemax = 9  ! is this number correct? check later
   if (patch%itype(p) >= nptreemax) then   ! if not tree
      ! for shrubs and herbs
      vcmax25top = lnc(p) * ( i_flnr(patch%itype(p)) + s_flnr(patch%itype(p)) * lnc(p) ) * fnr * act25 * &
           dayl_factor(p)
   else
      ! if tree
      vcmax25top = lnc(p) * ( i_flnr(patch%itype(p)) * exp(s_flnr(patch%itype(p)) * lnc(p)) ) * fnr * act25 * &
           dayl_factor(p)
      ! for trees
   end if
end if
```

Photosynthesis in the CLM model

```
if (c3flag(p)) then
   ! C3: Rubisco-limited photosynthesis
   ac(p,iv) = vcmax_z(p,iv) * max(ci-cp(p), 0._r8) / (ci+kc(p)*(1._r8+oair/ko(p)))

   ! C3: RuBP-limited photosynthesis
   aj(p,iv) = je * max(ci-cp(p), 0._r8) / (4._r8*ci+8._r8*cp(p))

   ! C3: Product-limited photosynthesis
   ap(p,iv) = 3._r8 * tpu_z(p,iv)

else

   ! C4: Rubisco-limited photosynthesis
   ac(p,iv) = vcmax_z(p,iv)

   ! C4: RuBP-limited photosynthesis
   aj(p,iv) = qe(p) * par_z * 4.6_r8

   ! C4: PEP carboxylase-limited (CO2-limited)
   ap(p,iv) = kp_z(p,iv) * max(ci, 0._r8) / forc_pbot(c)

end if
```

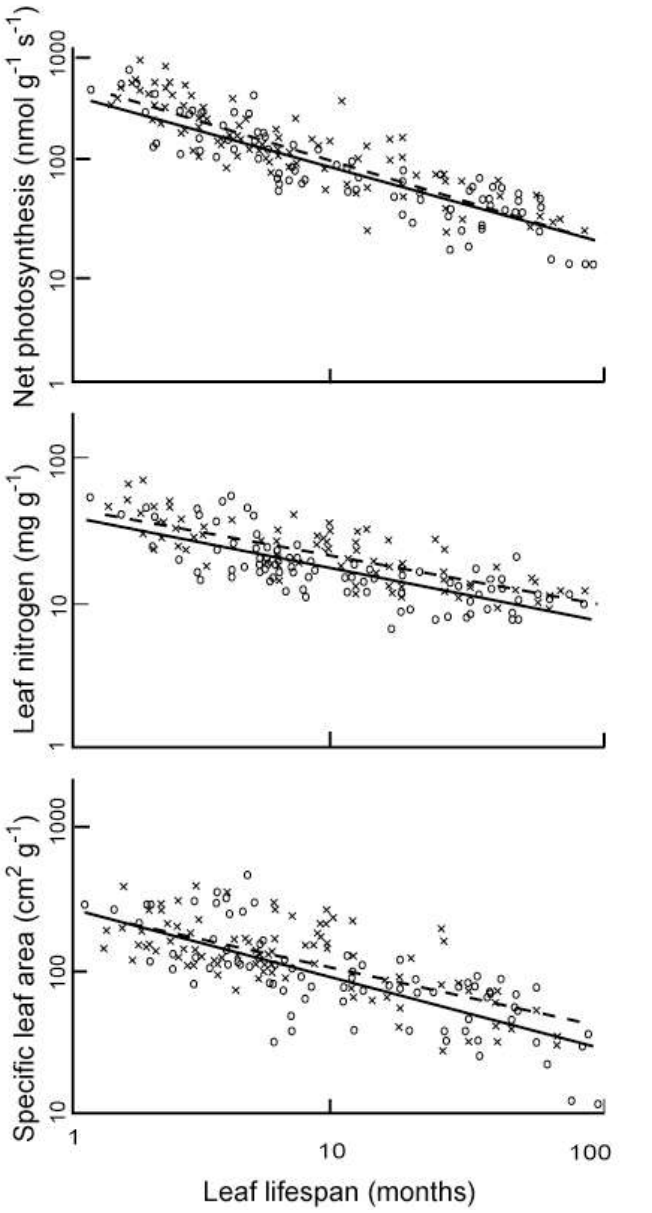
Main parameters in photosynthesis calculation

Parameter	Value	Explanation (Unit)
SLA	0.013	Specific leaf area ($m^2\ g^{-1}$ C)
CN_{leaf}	33	The base leaf carbon-to-nitrogen ratio (g C g^{-1} N)
F_{LNR}	0.055	Fraction of leaf nitrogen in Rubisco enzyme
F_{NR}	7.16	Mass ratio of total Rubisco molecular mass to nitrogen in Rubisco
a_{R25}	60	Specific activity of Rubisco (μmol CO_2 g^{-1} Rubisco s^{-1})
K_N	0.3	Leaf nitrogen decay coefficient for leaf to canopy scaling
LAI_Z	0~7	Leaf area index of each canopy layer ($m^2\ m^{-2}$)

Nitrogen limitation- tradeoffs

- Nitrogen limits leaf longevity
- High nitrogen content also increase plant respiration cost!

- **unavoidable trade-off between traits that maximize photosynthetic rate and traits that maximize leaf longevity**



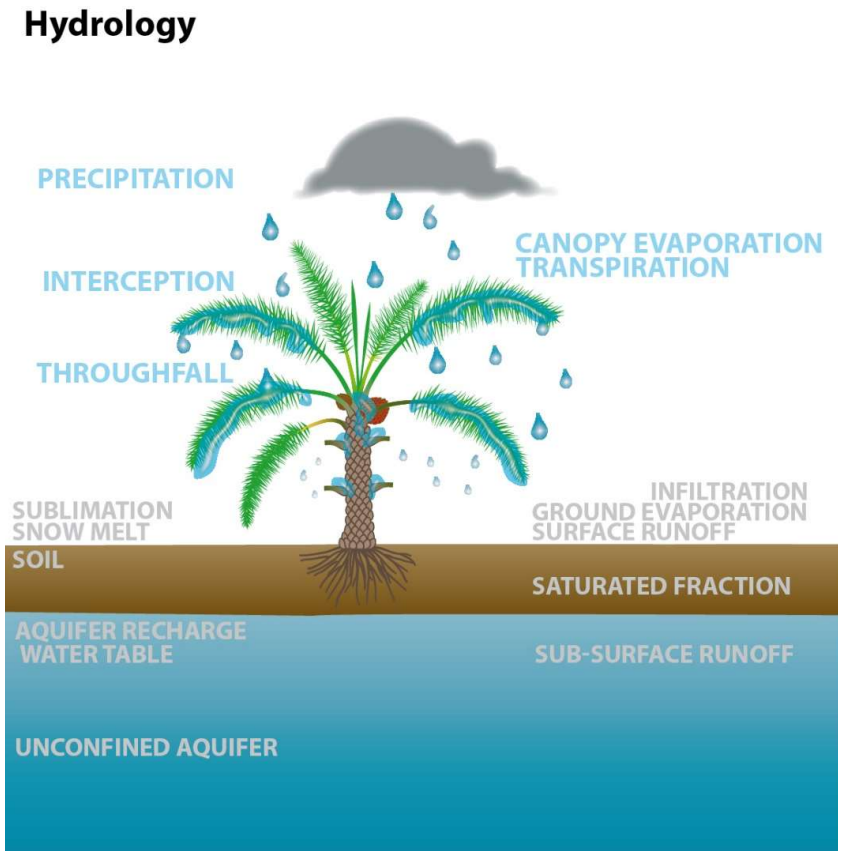
Chapin et al., 2011

Controls of carbon input, What is missing?

Water

Water stress- reduces the capacity of individual leaves to match CO_2 supply (stomata minimize water loss) with light availability

Excess water- intercepted canopy water blocks stomata and reduces transpiration and CO_2 supply



What are the controls of carbon input?

Leaf scale

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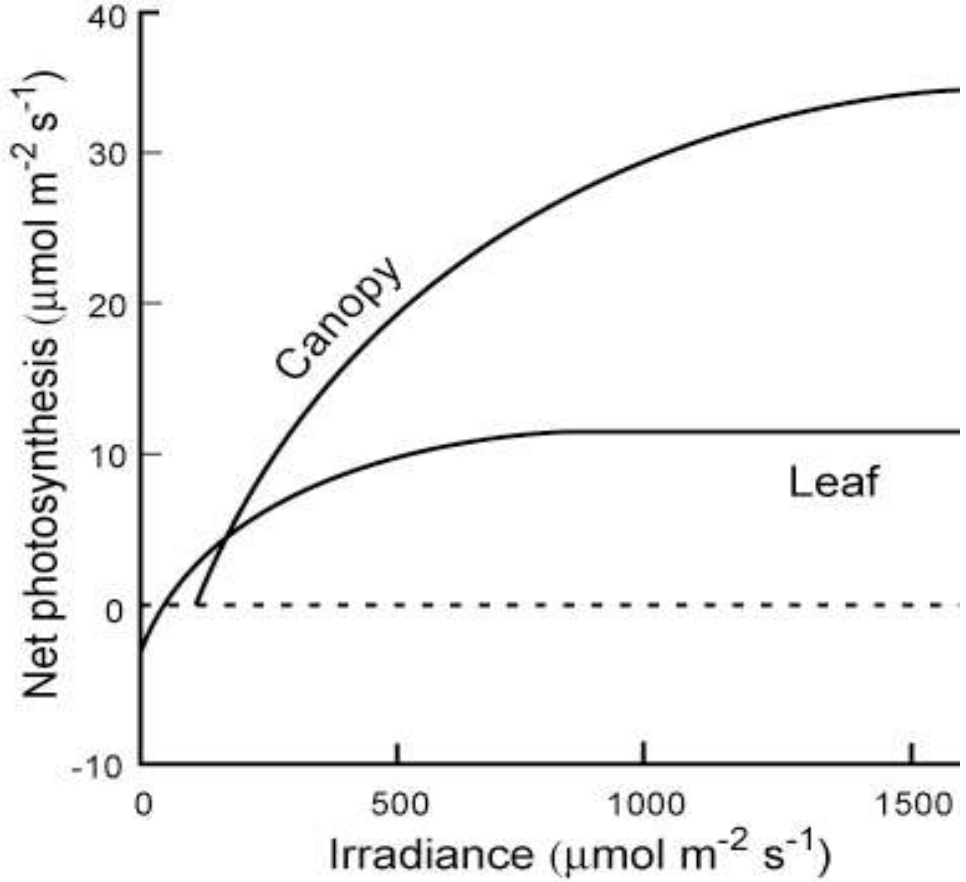
Ecosystem scale

Controls on leaf scale
+
Controls on canopy scale:
Leaf area
Photosynthetic season

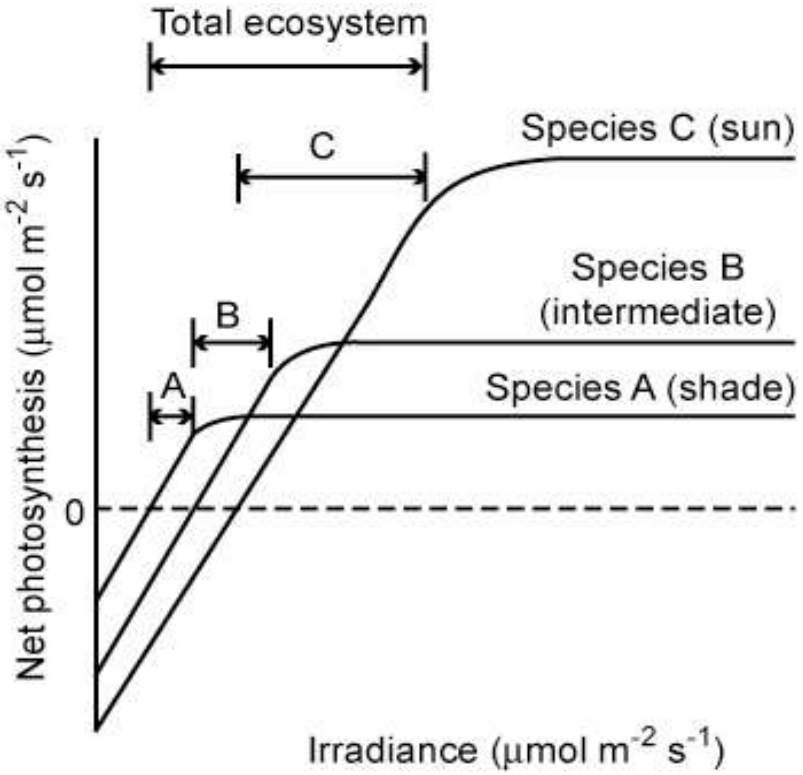
Review Question 3. How does each major environmental variable (CO2 , light, nitrogen, water, temperature, pollutants) affect photosynthetic rate in terrestrial plants in the short term? How do plants adjust to changes in each factor over the long term?

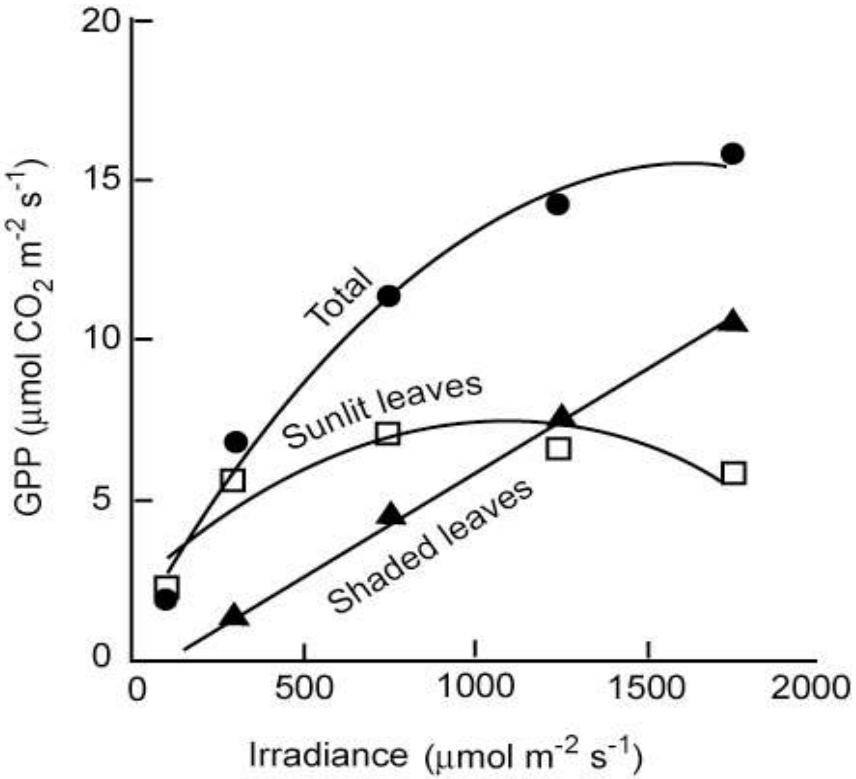
Canopy properties extend the range of light availability over which the light use efficiency (LUE) of the canopy remains constant (linear response)



-> higher saturation point

Chapin et al., 2011





Chapin et al., 2011

What are the controls of carbon input?

Leaf area

The availability of soil resources, especially water and nutrient supply, accounts for much of the spatial variation in leaf area and GPP among ecosystem types:

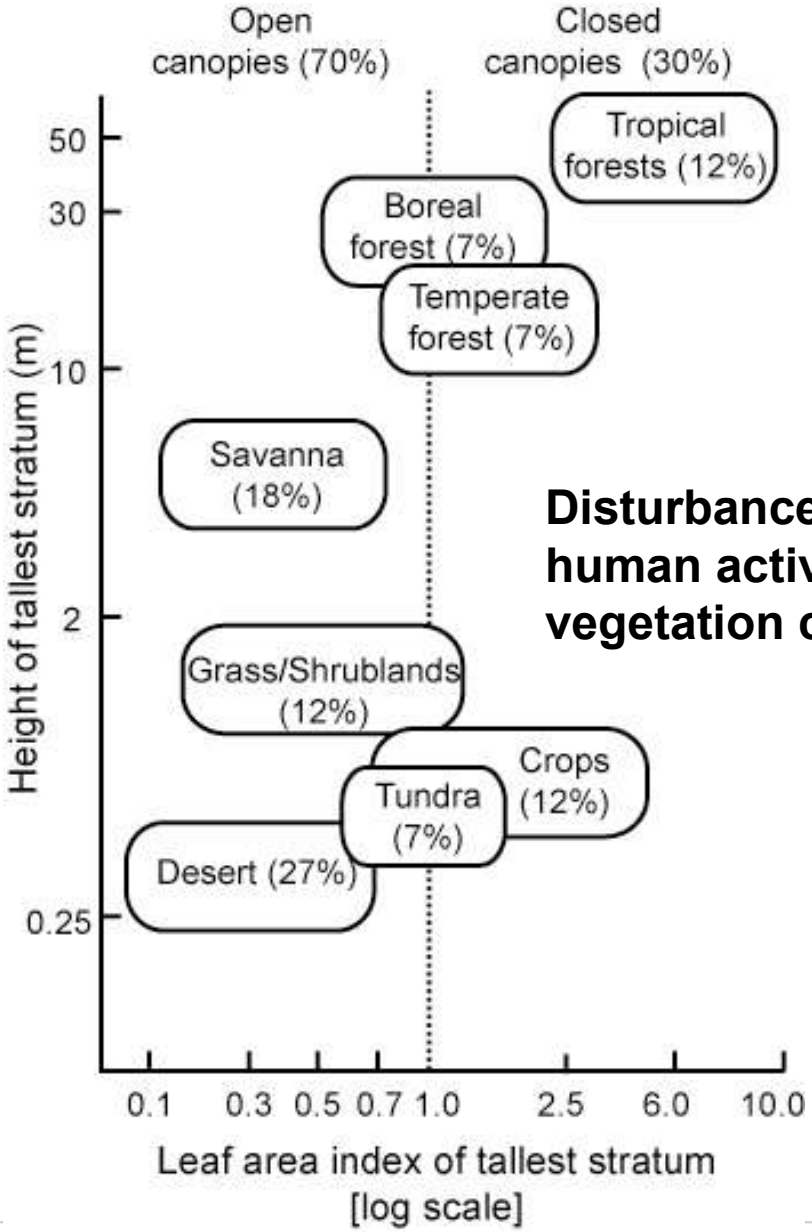
(1) Plants in high-resource environments produce a large amount of leaf biomass,

(2) leaves produced in these environments have a high SLA

Photosynthetic length

The length of the photosynthetic season accounts for much of the ecosystem differences in GPP.

Plant traits are adapted to climate to control photosynthetic length e.g. phenology (deciduous /evergreen /annual), morphology (resistance to disturbance), leaf longevity

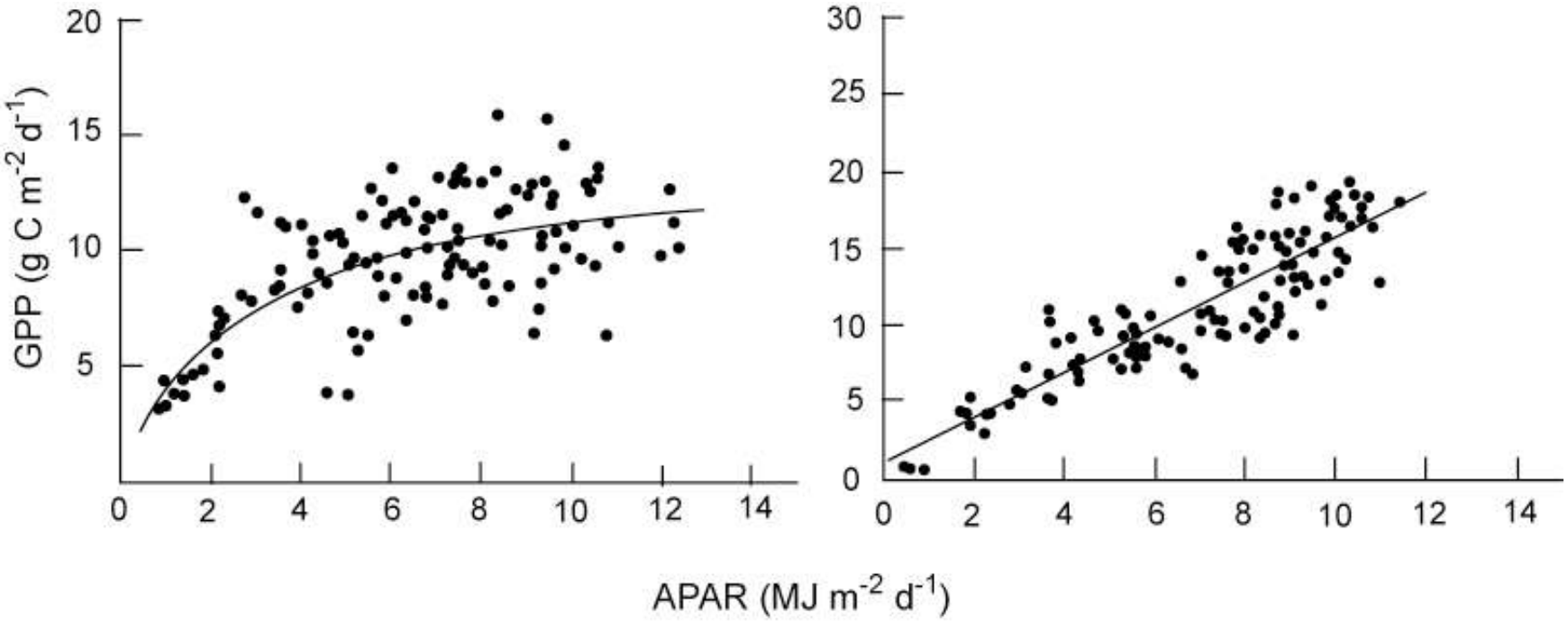


Disturbances, herbivory, pathogens and human activities (land use) reduce vegetation cover (LAI) and GPP

Chapin et al., 2011

Forest

Crop



Crops have higher water and nutrient availability

Chapin et al., 2011

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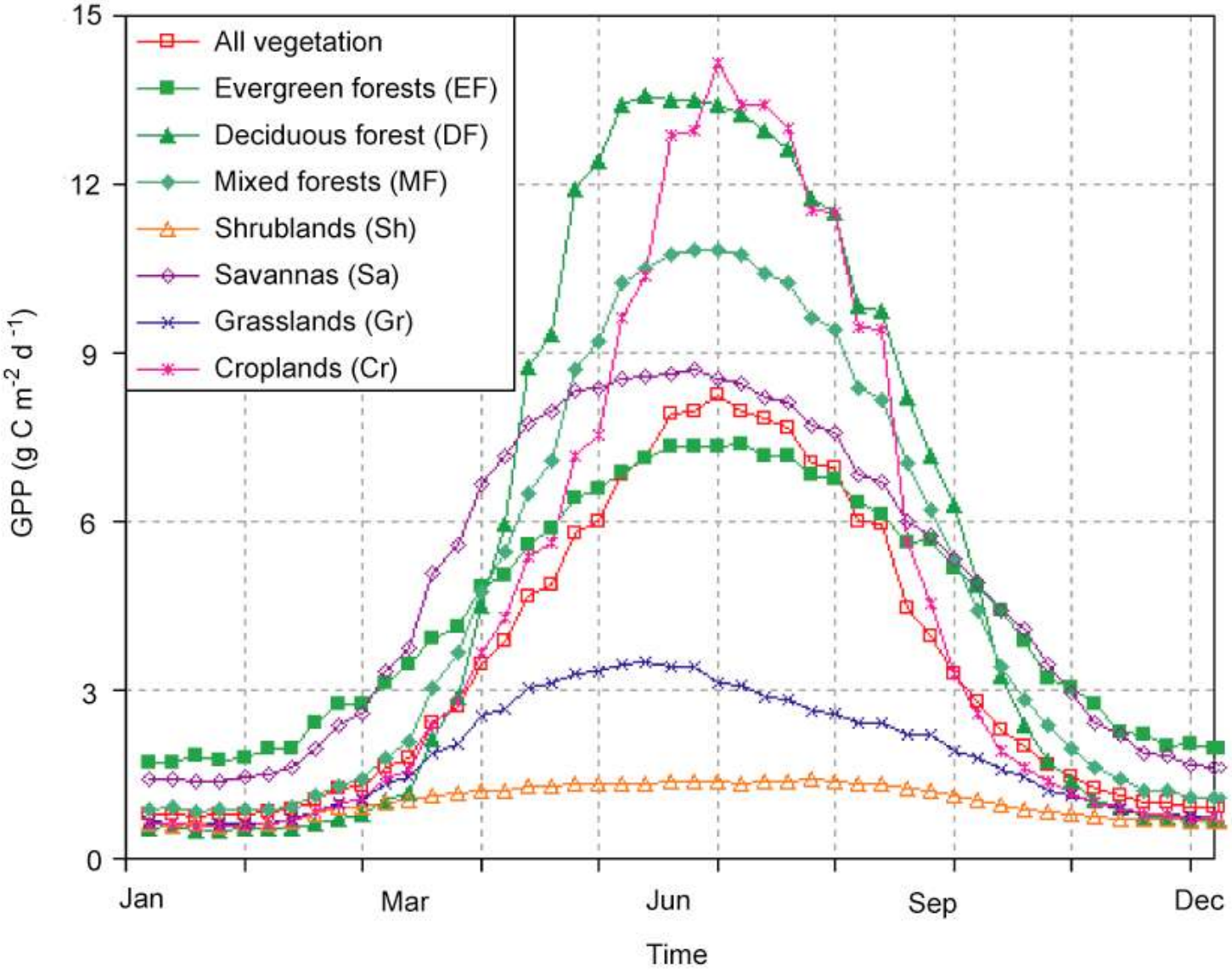
Photosynthetic length and GPP



Chapin et al., 2011

Summary

An important conclusion of leaf- and canopy-level studies of photosynthesis is that many factors cause convergence of ecosystems toward a **relatively similar efficiency of converting absorbed light energy into carbohydrates (LUE)**.

- All C3 plants have a similar quantum yield (LUE) at low to moderate irradiance.
- Penetration of light and vertical photosynthetic profile through a canopy extend the range of irradiance over which LUE remains relatively constant.

Summary

- In short term, LUE of a given ecosystem varies primarily in response to light intensity and environmental stresses (water stress) that reduce stomatal conductance.
- Over the long term, plants respond to environmental stresses by reducing leaf area and the concentrations of photosynthetic pigments and enzymes so photosynthetic capacity matches stomatal conductance (**balanced co-limitation**)

Overall, ecosystems producitivity is complex but measurable, with **processed-based modeling** (which represents these complex key leaf-to-canopy level processes) or with **remote sensing** (that captures the similar and predictable patterns, e.g. LUE x NDVI x PAR, among ecosystems)

Questions & discussions

Reiew question 6. What factors are most important in explaining differences among ecosystems in GPP? Over what time scale does each of these factors have its greatest impact on GPP?

Reiew question 8. How do the factors regulating photosynthesis in a forest canopy differ from those in individual leaves? How do availability of soil resources (water and nutrients) and the structure of the canopy influence the importance of these canopy effects?

Your questions?

References:

Chapin III, F.S., Matson, P.A., Vitousek, P., 2011. Principles of terrestrial ecosystem ecology. Springer Science & Business Media.

Fan, Y., Roupsard, O., Bernoux, M., Le Maire, G., Panferov, O., Kotowska, M.M., Knohl, A., 2015. A sub-canopy structure for simulating oil palm in the Community Land Model (CLM-Palm): phenology, allocation and yield. Geosci. Model Dev. 8, 3785–3800. doi:10.5194/gmd-8-3785-2015

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