Feb 5, 2024

Biophysical Models and Applications in Ecosystem Analysis

Modeling Ecosystem Production (Chapter 2)

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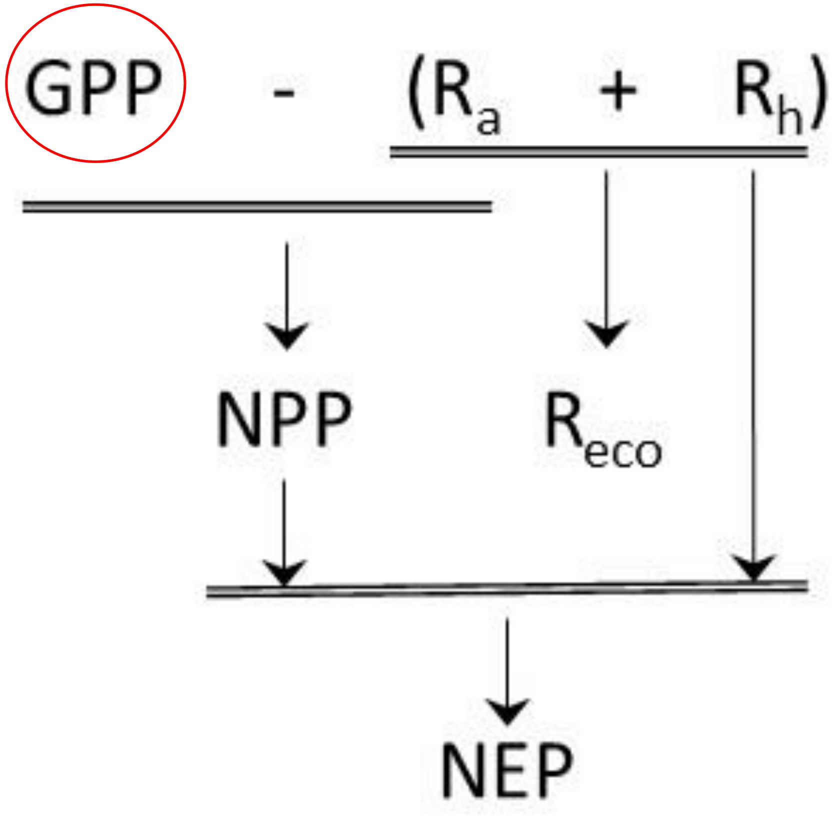


Soil respiration (Rs)

Photosynthesis is the first step for assimilating atmospheric CO_2 into organic substances in an ecosystem

- Photosynthesis is a physiological process in which plants, algae and certain bacteria convert solar energy and CO_2 to chemical energy and carbohydrate – such as glucose, sugar, and cellulose.

- “Photosynthesis’ is a combination of the Greek words “light" and "putting together".

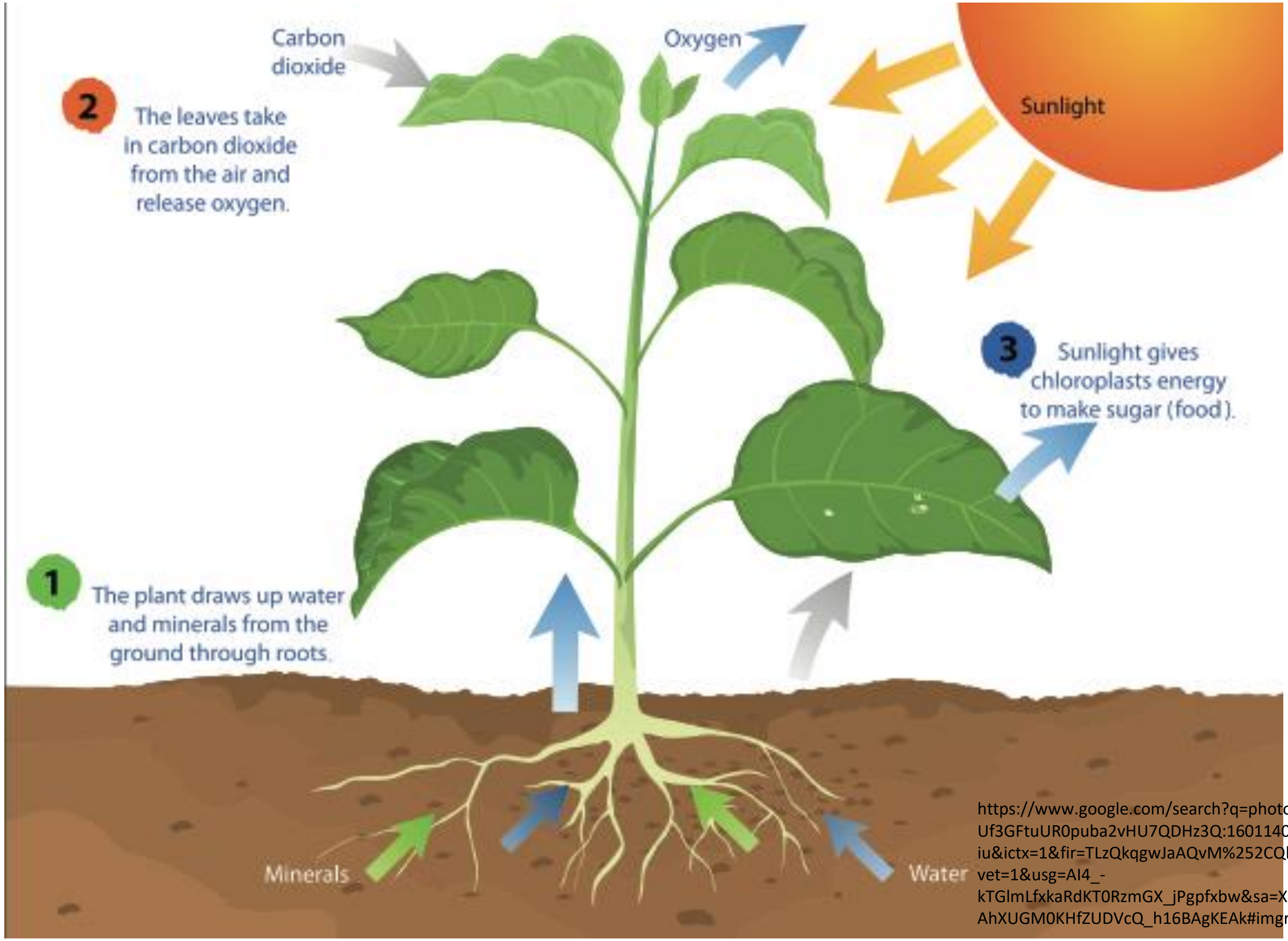
- The process was discovered by Dutch physician Jan Ingenhousz in the late 1700s

- Chemical conversions take place with Chlorophyll a.

- Two types of chlorophyll pigments absorb light in the blue and red part of the visible spectrum

Plants use sunlight, water, and the gases in the air to make glucose, which is a form of sugar that plants need to survive.

https://www.youtube.com/watch?v=FfLLHQDgpjI



https://www.google.com/search?q=photosynthesis&sxsrf=ALeKk
Uf3GFtuUR0puba2vHU7QDHz3Q:1601140211398&tbm=isch&sou
iu&ictx=1&fir=TLzQkqgwJaAQvM%252CQhH9beDDf9MhbM%252
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AhXUGM0KHfZUDVcQ_h16BAgKEAk#imgrc=TLzQkqgwJaAQvM

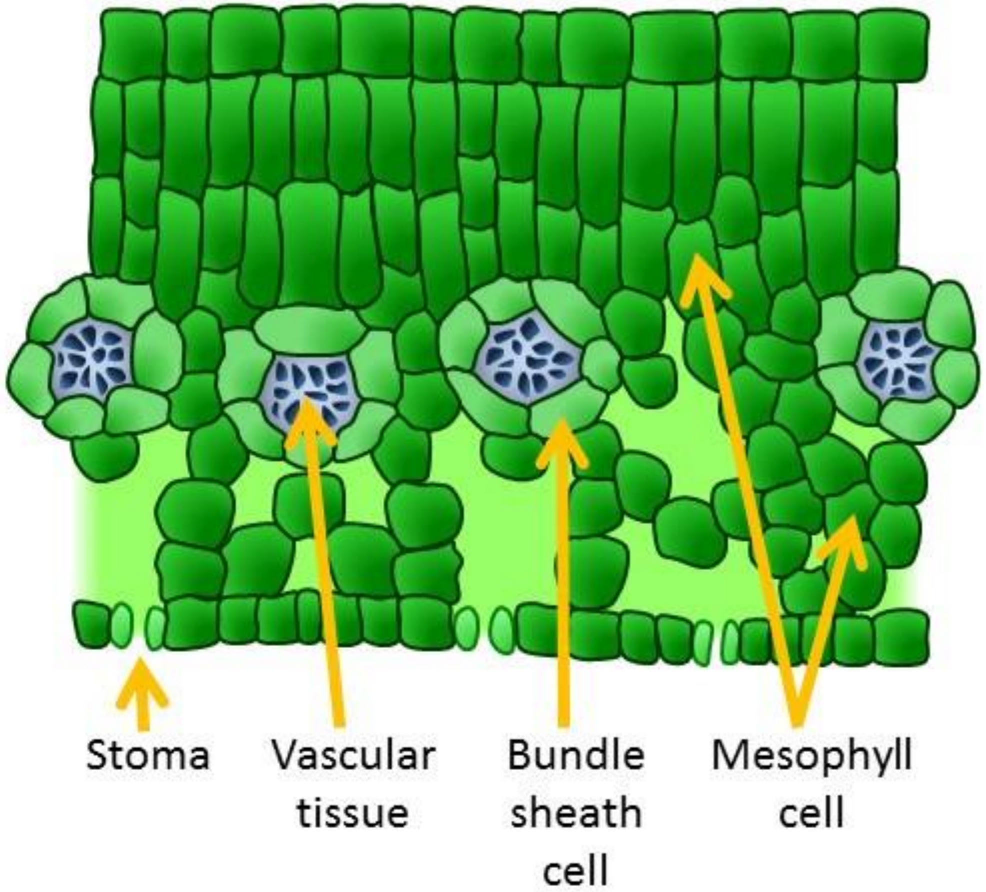
Chemical expression has several forms, including the following one:

$$6CO_2 + 12H_2O + \text{Solar Energy} \rightarrow C_6H_{12}O_6 + 6O_2 + 6H_2O$$

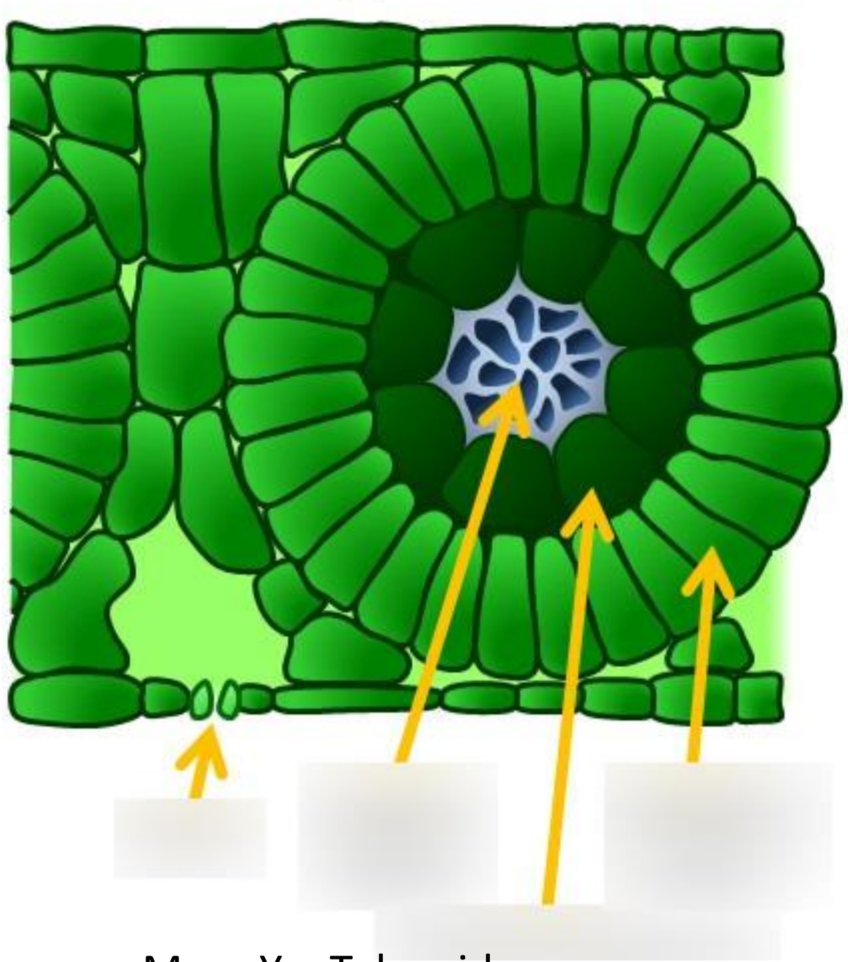
Comparing C3, C4 and CAM

https://www.youtube.com/watch?v=13h5oC4jIsk

C_3 plant



C_4 plant



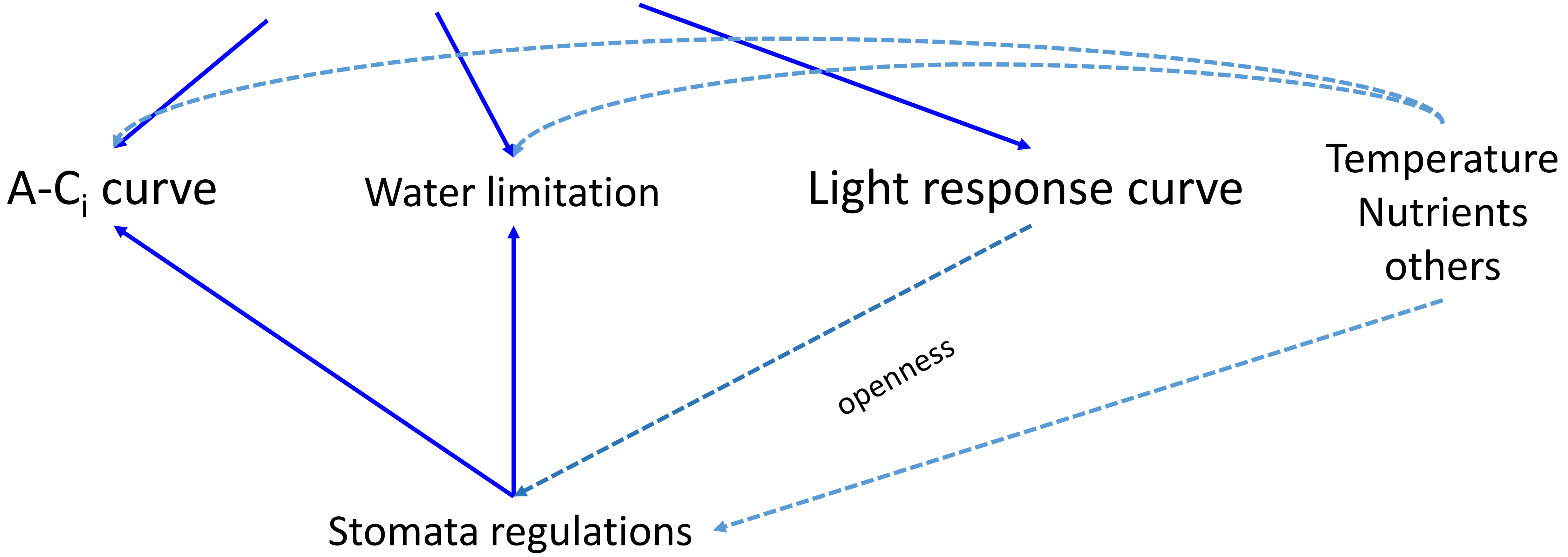
CAM

More YouTube videos:
https://www.youtube.com/watch?v=HbLg4lMpUa8
https://www.youtube.com/watch?v=Dq38MpYOb8w

https://quizlet.com/ca/341425087/c4-plants-diagram/

Chemical expression has several forms, including the following one:

$$6CO_2 + 12H_2O + \text{Solar Energy} \xrightarrow{\text{enzyme}} C_6H_{12}O_6 + 6O_2 + 6H_2O$$



Measuring photosynthesis: chamber-based at leaf level (snapshots)

LiCor6400 (LI6800)

CO_2 & H_2O concentration

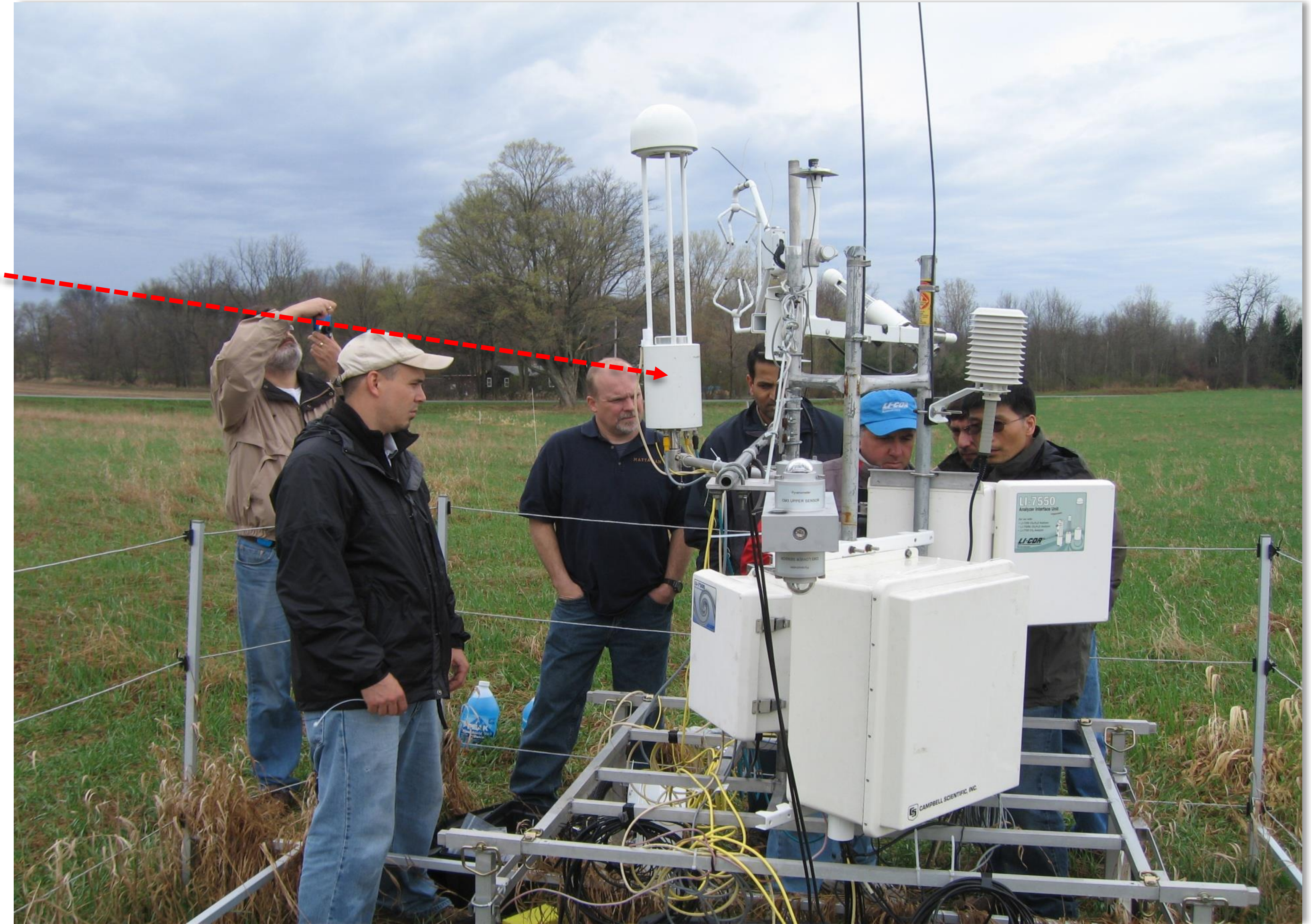
PAR, temperature

Measuring photosynthesis: chamber-based at leaf level (continuous)

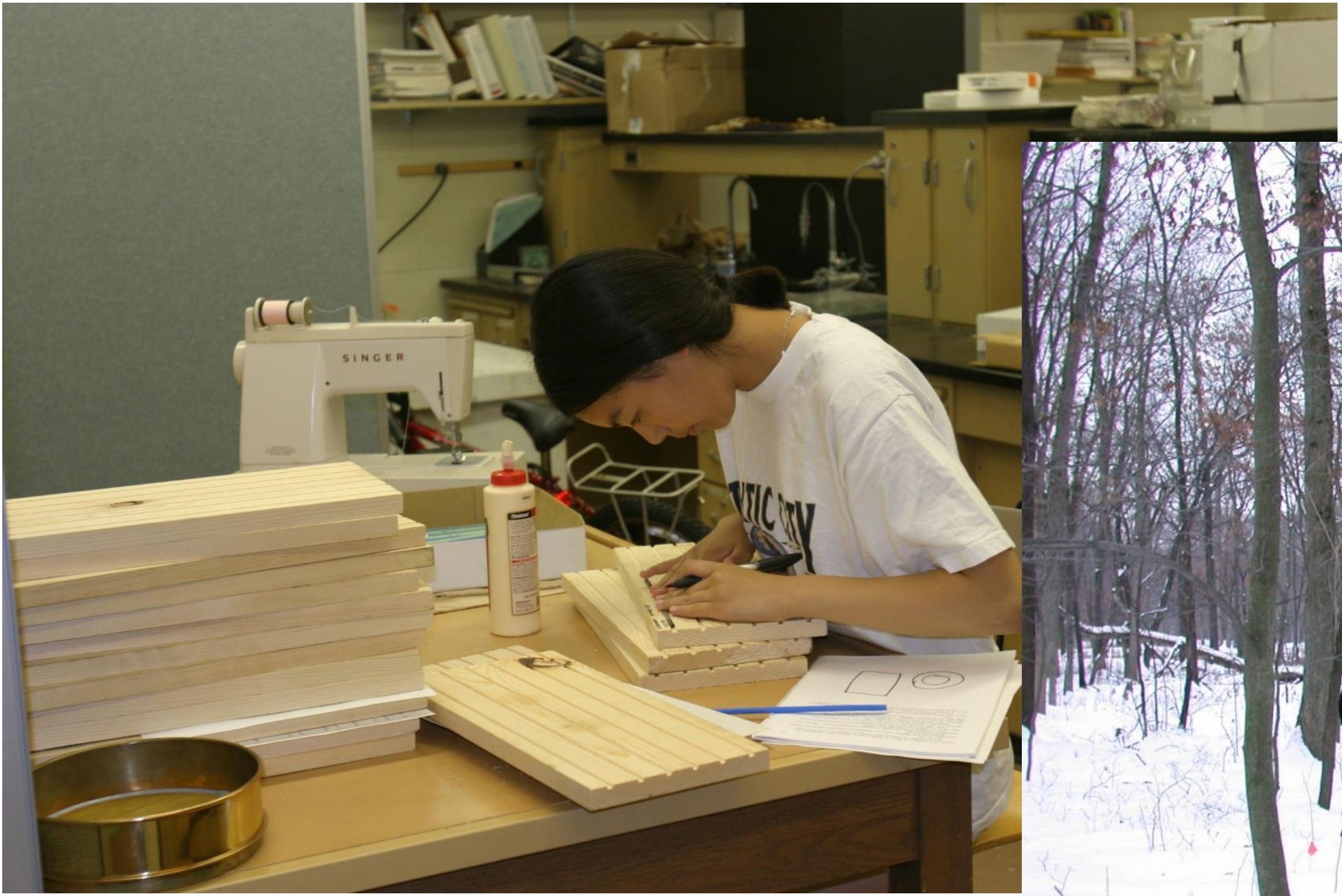
Measuring photosynthesis: EC tower

Open-path EC tower
daytime minus nighttime
(NEE = GEP – R_{eco})

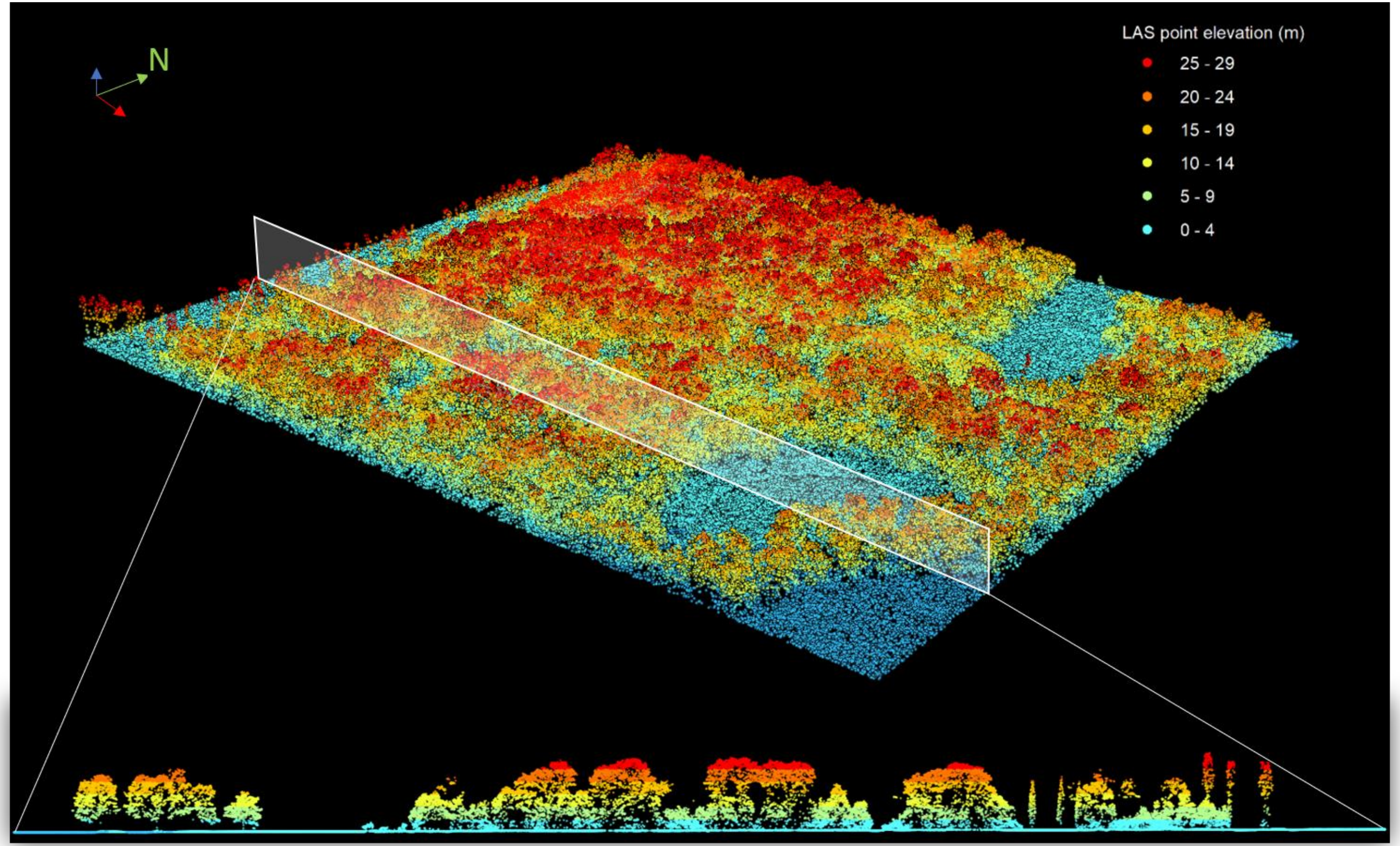
LI7700
CH_4



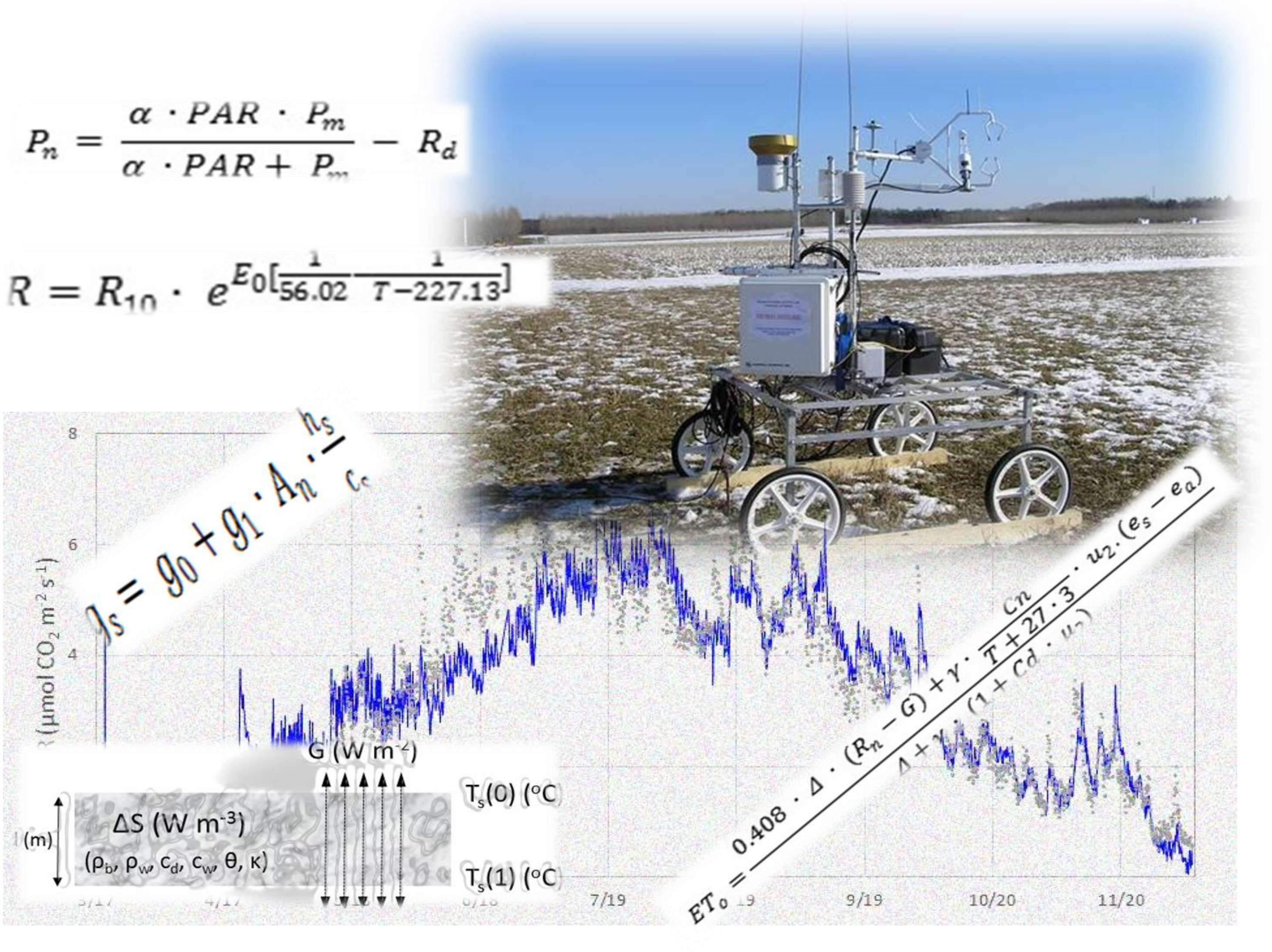
Measuring photosynthesis: Biometric approach (tree ring, DBH)



Measuring photosynthesis: remote sensing modeling



Measuring photosynthesis: ecosystem modeling



2.2 Core biophysical Models for Ecosystem Production

2.2.1 Michaelis-Menten model

2.2.2 Landsberg model

2.2.3 Farquhar's model

2.2.4 Photosynthesis based on stomatal conductance (g_s)

2.2.6 Light use efficiency (LUE) model

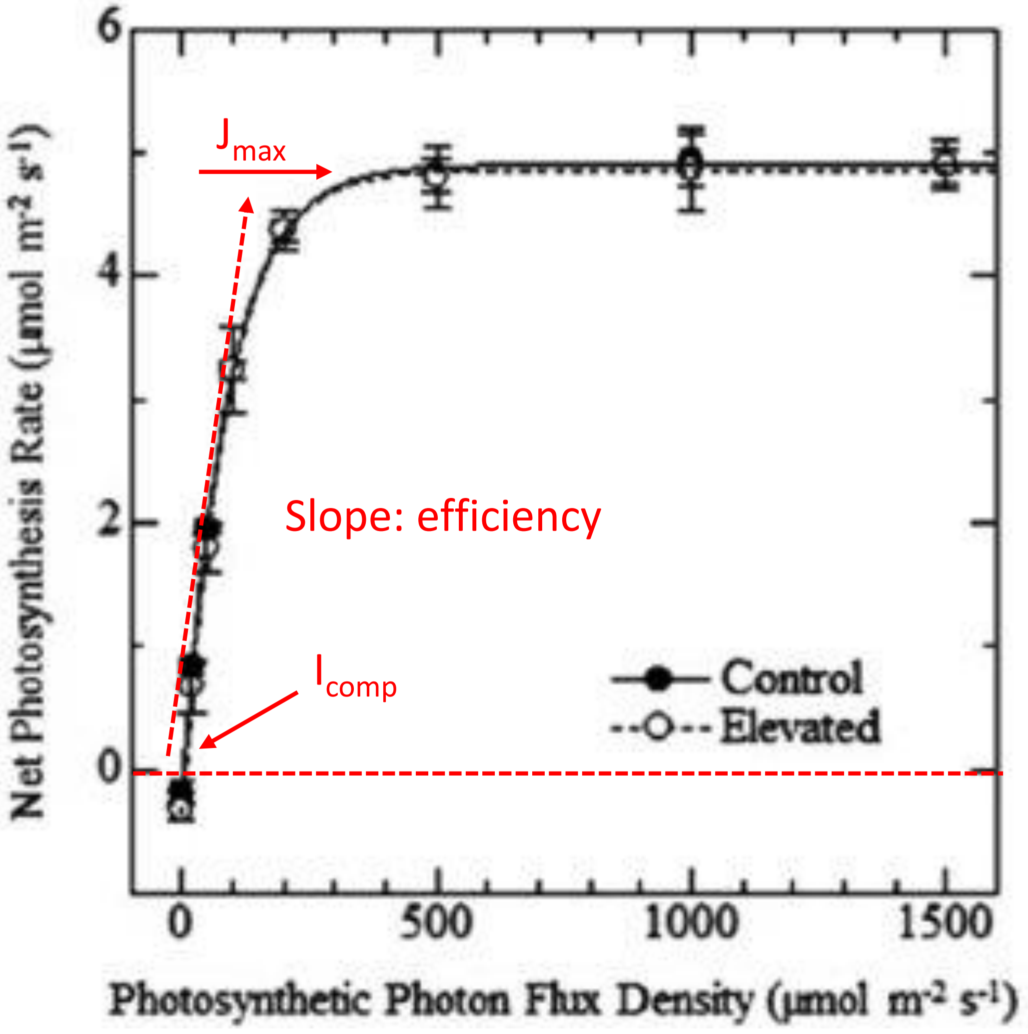
2.2.7 Nitrogen use efficiency (NUE) model

2.2.8 Water use efficiency (WUE) model

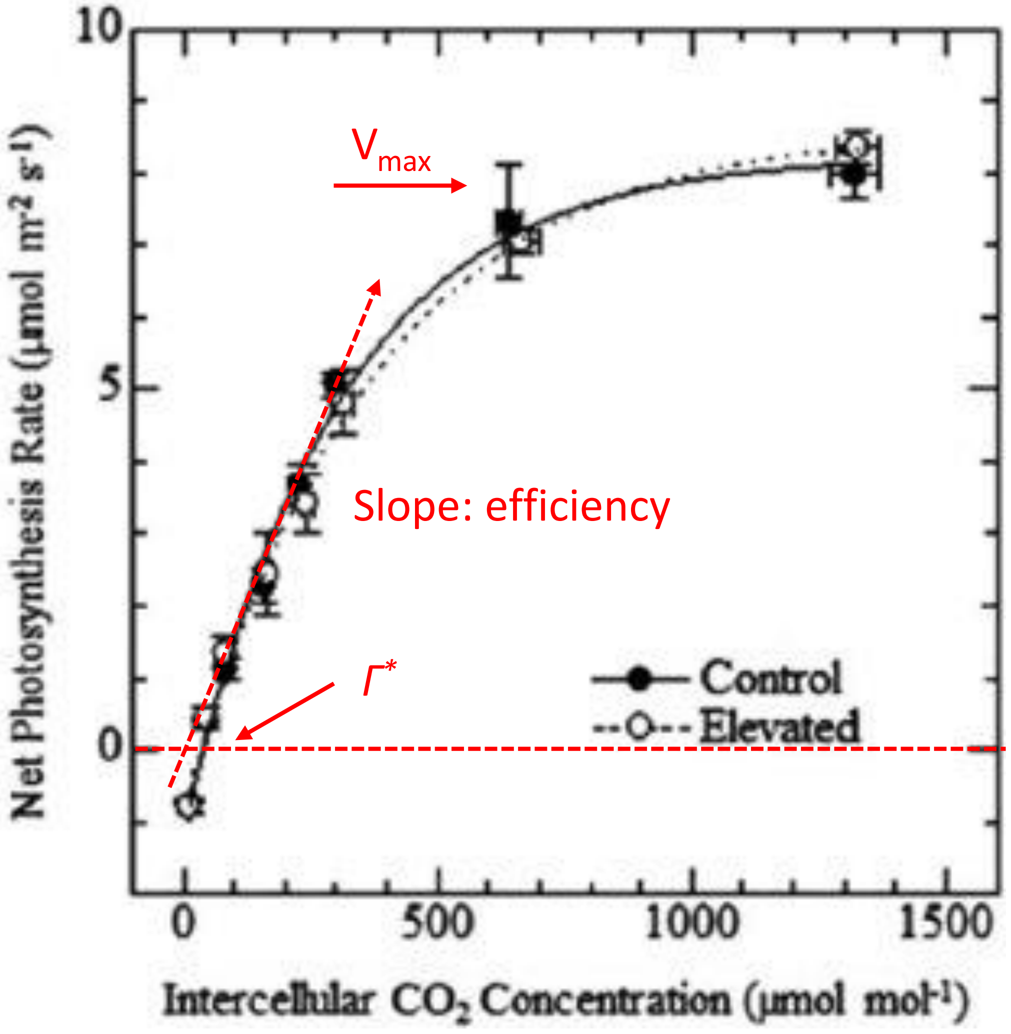
Major variables and Symbols

Pn/An:	Photosynthesis rate (μmol m^{-2} s^{-1})
PAR (PPFD):	photosynthetically active radiation (μmol m^{-2} s^{-1})
VPD:	vapor pressure deficit (kPa)
I_o or I_{comp}	light compensation point (μmol m^{-2} s^{-1})
Γ^*:	CO_2 compensation point (ppm)
P_{max}/A_{max}:	maximum Pn or A (μmol m^{-2} s^{-1})
V_{max}:	maximum Pn under CO2 limited (μmol m^{-2} s^{-1})
J_{max}:	maximum Pn under light limited (μmol m^{-2} s^{-1})
g_s:	Stomata conductance (μmol m^{-2} s^{-1})

1. Light response curve



2. A-C_i curve

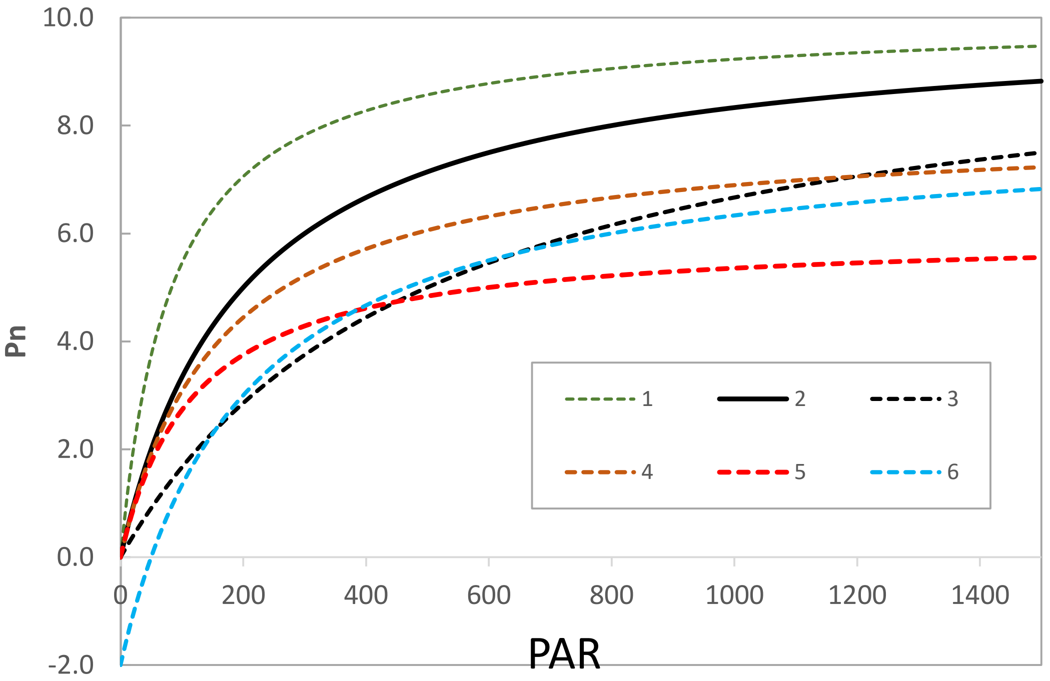


https://www.researchgate.net/publication/263642910_Effects_of_Elevated_CO2_Concentration_and_Temperature_on_Physiological_Characters_of_Liriodendron_tulipifera/figures?lo=1

2.2.1 Michaelis-Menten model

$$P_n = \frac{\alpha \cdot PAR \cdot P_m}{\alpha \cdot PAR + P_m}$$

Michaelis constant (K_m) of the enzyme is an inverse measure of affinity. K_m is the value when P_n reaches half of the P_m.



Line	α	P_m	R_d
1	0.12	10	0
2	0.05	10	0
3	0.02	10	0
4	0.05	8	0
5	0.05	6	0
6	0.05	10	2

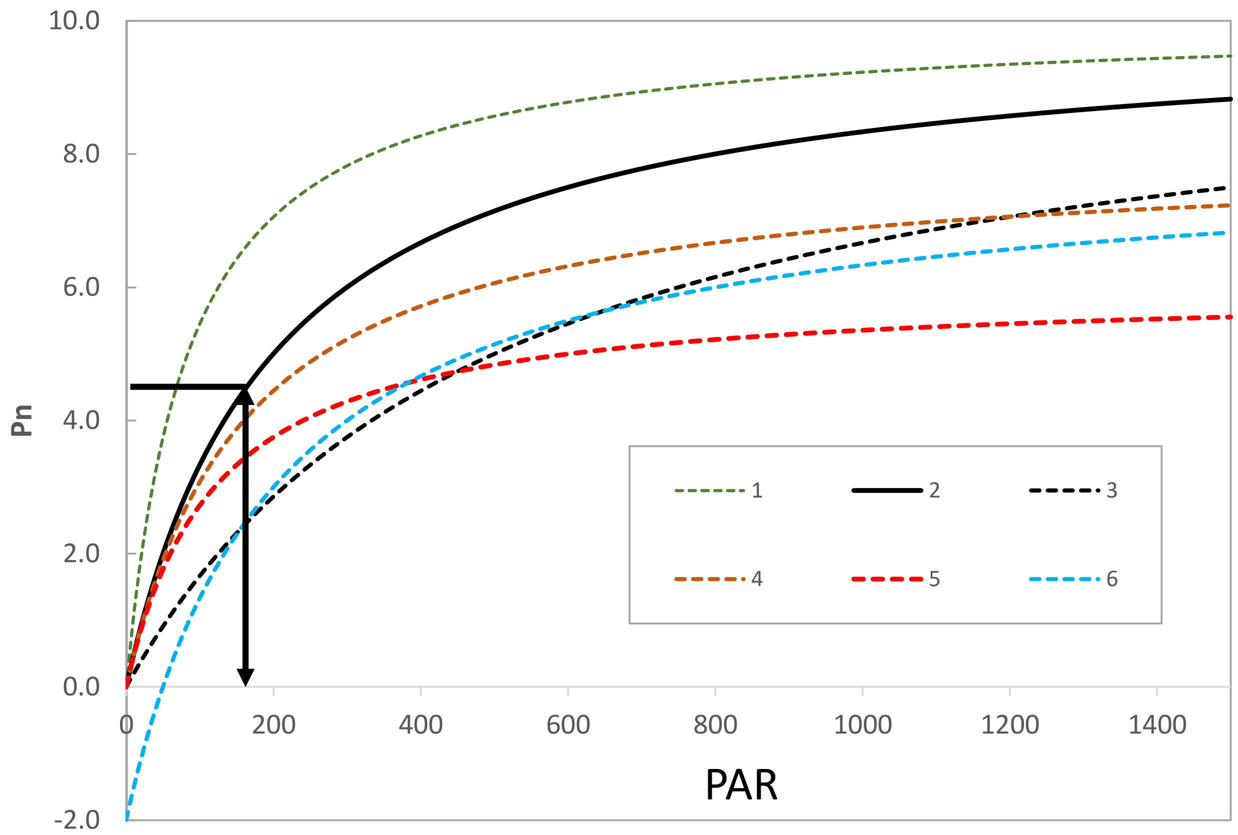
MM model with Respiration (R_d)

$$P_n = \frac{\alpha \cdot PAR \cdot P_m}{\alpha \cdot PAR + P_m} - R_d$$

2.2.1 Michaelis-Menten model

$$P_n = \frac{\alpha \cdot PAR \cdot P_m}{\alpha \cdot PAR + P_m}$$

Michaelis constant (K_m) of the enzyme is an inverse measure of affinity. K_m is the value when P_n reaches half of the P_m.

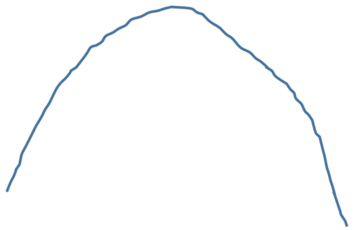


Michaelis Constant (K_m)

2.2.1 Michaelis-Menten model

Landsberg & Sands (2011) introduced an additional shape factor (β) into a non-rectangular hyperbolic model

$$P_n = p_m \cdot \frac{2 \cdot \alpha \cdot PAR/p_m}{1 + \alpha \cdot \frac{PAR}{Pm} + \sqrt{\left(1 + \alpha \cdot \frac{PAR}{Pm}\right)^2 - 4 \cdot \alpha \cdot \beta \cdot PAR/p_m}}$$



$Y=a+b*x + c*X^2$

This model is virtually the same as Eq. 2.1 when β = 0. The value of β should be less than 1 for simulations.

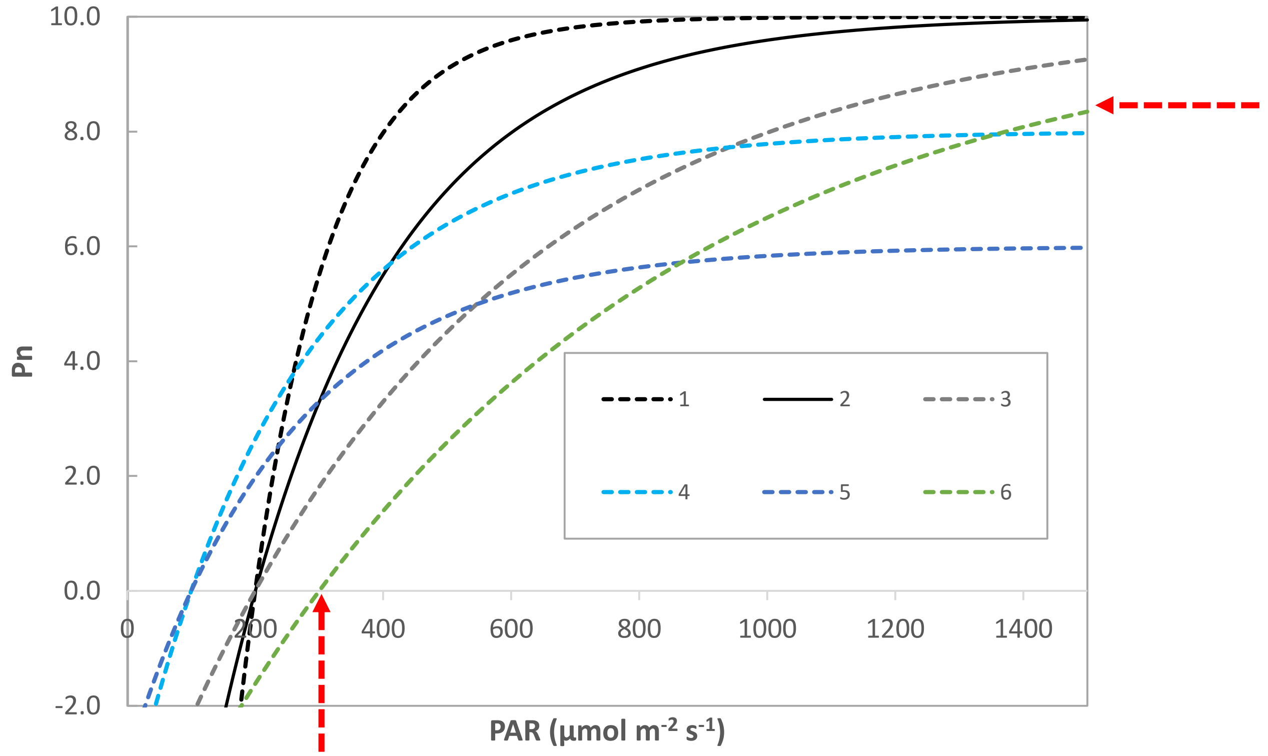
An alternative expression of the non-rectangular hyperbolic model is applied by Peat (1970) as:

$$P_n = \frac{1}{2 \cdot \beta}\left(\alpha \cdot PAR + P_m - \sqrt{(\alpha \cdot PAR + P_m)^2 - 4 \cdot \alpha \cdot PAR \cdot P_m \cdot \beta}\right)$$

2.2.2 Landsberg model

$$P_n = P_m \cdot \left(1 - e^{\alpha \cdot (PAR - I_{comp})}\right)$$

Line	α	P_m	I_{comp}
1	0.008	10	200
2	0.004	10	200
3	0.002	10	200
4	0.004	8	100
5	0.004	6	100
6	0.002	10	300



In-class exercise

- Create a spreadsheet model for MM and Landsberg model to explore the sensitivity of each parameters.
- PAR values vary from 0 to 2000 (μmol m^{-2} s^{-1})

2.2.3 Farquhar's model

Photosynthesis rate for Rubisco-limited, RuBP-limited, and product-limited assimilations (A_c, A_j, and A_p).

Ac as a function of intercellular CO_2 concentration is described by FvCB equation:

$$A_c = \frac{V_{max} \cdot (c_i - \Gamma^*)}{c_i + K_c \cdot (1 + \frac{O_i}{K_O})}$$

V_{max} is the maximum activity of Rubisco

c_i is the intercellular CO_2 concentration (μmol mol^{-1}),

Γ^* is the CO_2 compensation point in the absence of day respiration (R_d),

K_c is the Michaelis-Menten constant of Rubisco for CO_2,

O_i is the oxygen (O_2) concentration in the atmosphere (209 mol mol^{-1}),

K_o is the Michaelis-Menten constant of Rubisco for O_2.

2.2.3 Farquhar's model

Γ^* is calculated as:

$$\Gamma^* = \frac{0.5 \cdot O_i}{2600 \cdot 0.57^{Q10}}$$

K_c for CO_2 is calculated as:

$$K_c = 30 \cdot 2.1^{Q10}$$

K_o for O_2 is calculated as:

$$K_c = 30000 \cdot 1.2^{Q10}$$

2.2.3 Farquhar's model

RuBP-limited photosynthesis rate (A_j), also commonly known as light-limited photosynthesis rate, is calculated as:

$$A_j = \frac{\mathrm{J} \cdot (c_i - \Gamma^*)}{4 \cdot c_i + 8 \cdot \Gamma^*}$$

j is the electron transport rate (µmol m^{-2} s^{-1}) and varies with absorbed photosynthetically active radiation (*aPAR*).

Finally, the product-limited photosynthesis rate is calculated as:

$$A_p = 3 \cdot T_p$$

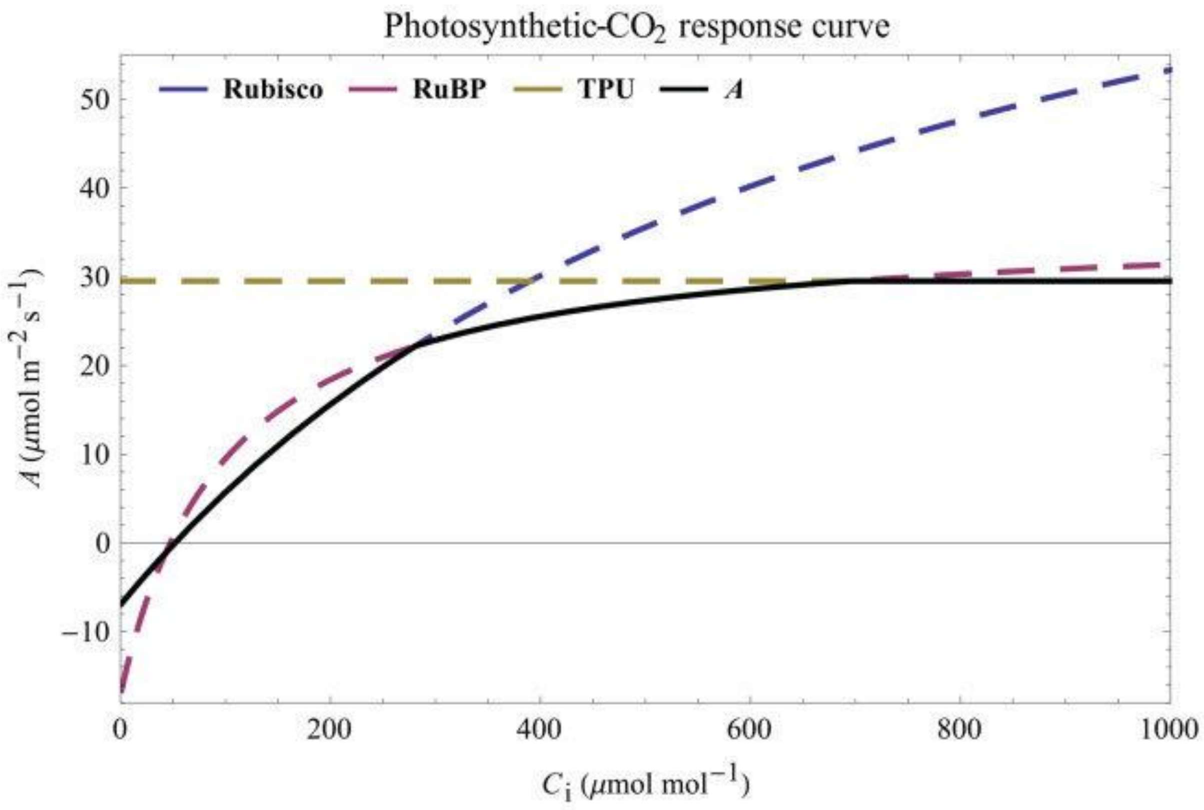
T_p (µmol m^{-2}) is the triose phosphate utilization rate. This rarely limits the rate of photosynthesis under physiological conditions

2.2.3 Farquhar's model

A_n is the least of the three rates: $A_n = minimum(A_c, A_j, A_p)$

The four major parameters that are needed to fit Farquhar's model

V_{max} (μmol m^{-2} s^{-1}),
J_{max} (μmol m^{-2} s^{-1}),
T_p (μmol m^{-2} s^{-1})
R_d (μmol m^{-2} s^{-1})



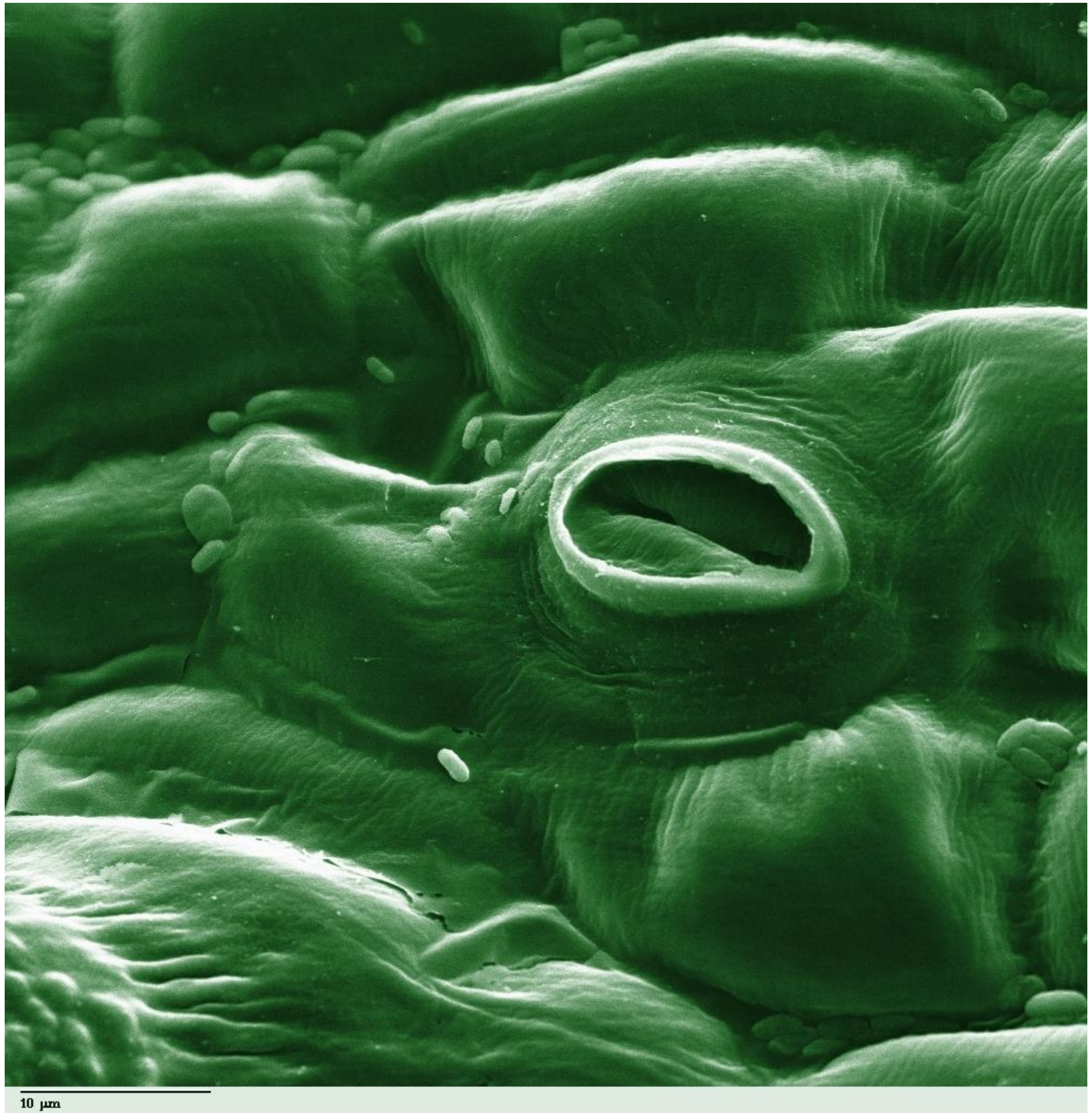
https://www.researchgate.net/publication/236199968_Modeling_C3_photosynthesis_from_the_chloroplast_to_the_ecosystem/figures?lo=1

Web Sources for A models

https://biocycle.atmos.colostate.edu/shiny/photosynthesis/
https://leafweb.org/

2.2.4 Photosynthesis based on stomatal conductance (g_s)

- The diffusion rate is called stomatal conductance (g_s, μmol m^{-2} s^{-1}), which is proportional to the photosynthesis rate (A_n, μmol m^{-2} s^{-1}).
- This linear relationship is modulated by leaf surface CO_2 and H_2O concentration and varies among leaves and species.



Ball-Berry model:

$$g_s = K \cdot A_n \cdot \frac{h_s}{c_s}$$

- h_s (ranging 0-1) is the fractional relative humidity at the leaf surface,
- c_s (μmol mol^{-1}) is the CO_2 concentration of leaf surface,
- K is the slope constant of the model that represents the composite sensitivity of g_s to CO_2 concentration

2.2.4 Photosynthesis based on stomatal conductance (g_s)

By reversing Eq. 2.13, photosynthesis is modeled as:

$$A_n = \frac{g_s \cdot c_s}{K \cdot h_s}$$

Stomata do not completely close, there is a minimum conductance value (g_o, mol m^{-2} s^{-1}). The Ball-Berry model is also expressed as:

$$g_s = g_0 + g_1 \cdot A_n \cdot \frac{h_s}{c_s}$$

2.2.4 Photosynthesis based on stomatal conductance (g_s)

Leuning (1990) argued that the use of $[c_s - \Gamma]$ is more appropriate in the numerator, and he modified the original Ball-Berry model:

$$g_s = g_0 + \frac{a_1 \cdot A_n}{(c_s - \Gamma)}$$

Leuning reasoned this new form was applicable because $A_n \rightarrow 0$ when $c_s \rightarrow \Gamma$, rather than when $c_s \rightarrow 0$. With this model, the supply-constraint model of photosynthesis can be expressed as:

$$A_n = \frac{g_0}{1.6 \cdot (c_s - c_i) - g_{1 \cdot h_s} \cdot (c_s - \Gamma)}$$

2.2.4 Photosynthesis based on stomatal conductance (g_s)

Later, Leuning *et al.* (1995) made an additional modification to the model (Eq. 2.18) for C_3 plants as:

$$g_s = g_0 + \frac{a_1 \cdot A_n}{(c_s - \Gamma)(1 + \frac{D_s}{D_0})}$$

where D_0 is the value of *VPD* at which stomatal conductance becomes zero.

Lloyd (1991) proposed that g_s is dependent of $\sqrt{D}$. Medlyn *et al.* (2011) further emphasized the importance of g_1 in the Ball-Berry model because of its sensitivity to environmental changes (*e.g.*, temperature, soil water and nutrients). They also agreed with Leuning *et al.* (1995) that *VPD*, instead of relative humidity, should be used in modeling [$A_n \sim g_s$] for a new form of:

$$g_s = g_0 + 1.6 \cdot (1 + \frac{g_1}{\sqrt{D}}) \cdot \frac{A_n}{c_s}$$

Figure 2-4. Simulations of stomatal conductance (g_s) with different sets of parameters (Eq. 2.13). Other curves can be generated by altering parameters in **S2-2**

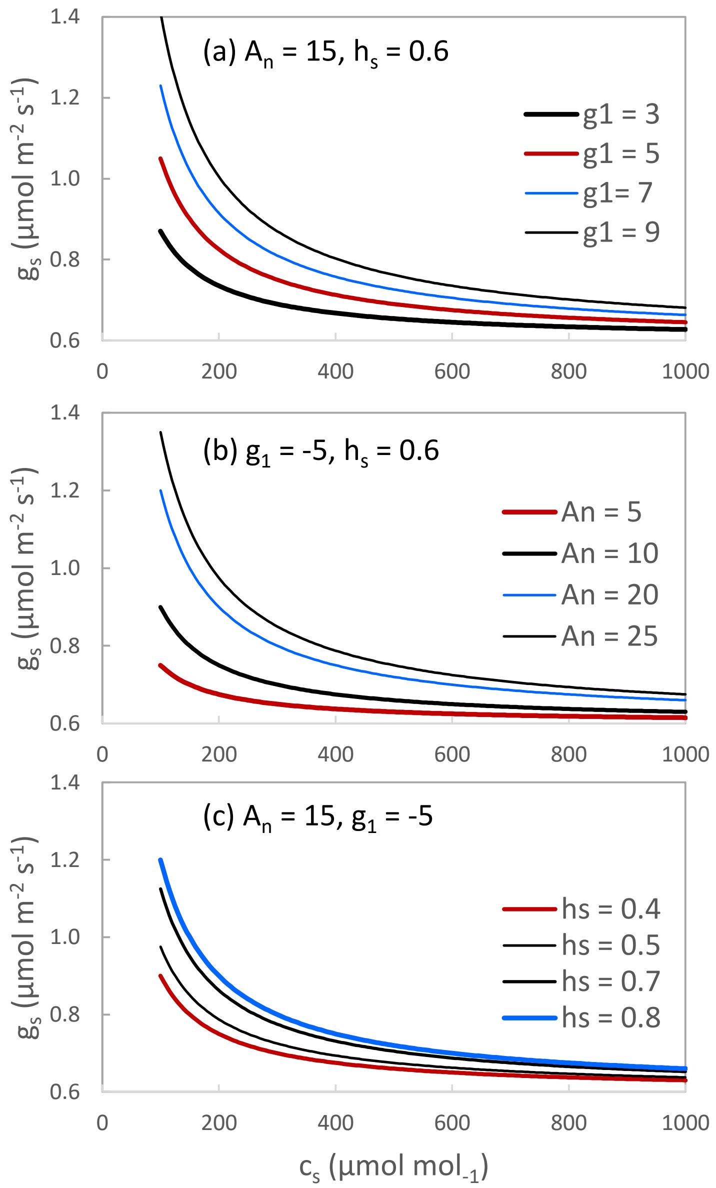


Figure 2-6. Changes in photosynthesis rate (A_n) with photosynthetically active radiation (*PAR*) (a) and CO_2 concentration (c_a) (b) for two species in Wang *et al.* (2018) (data use permission received from the authors).

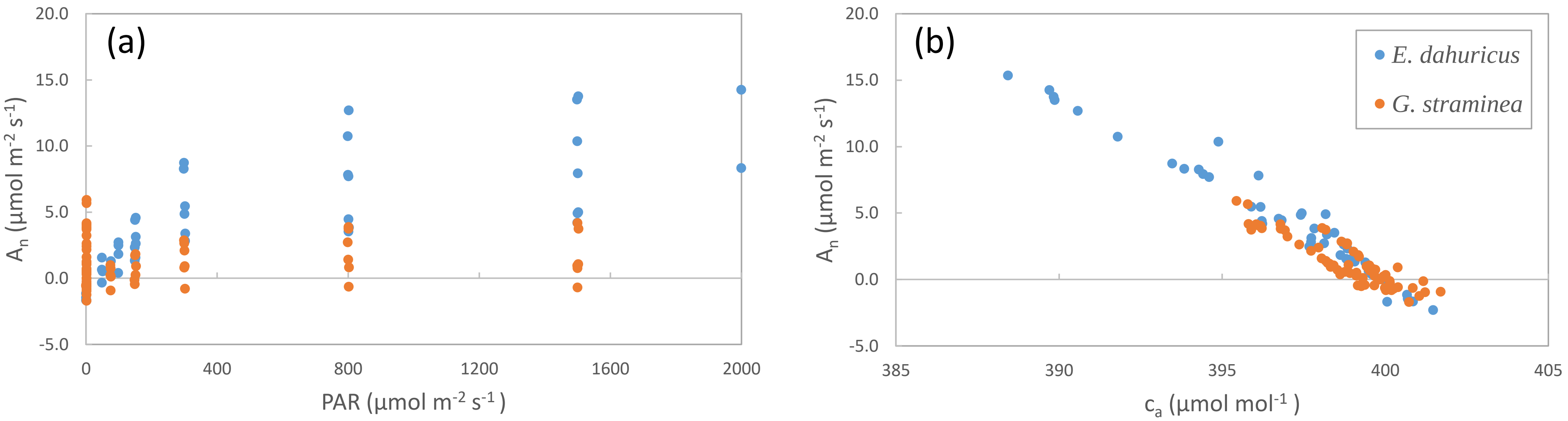
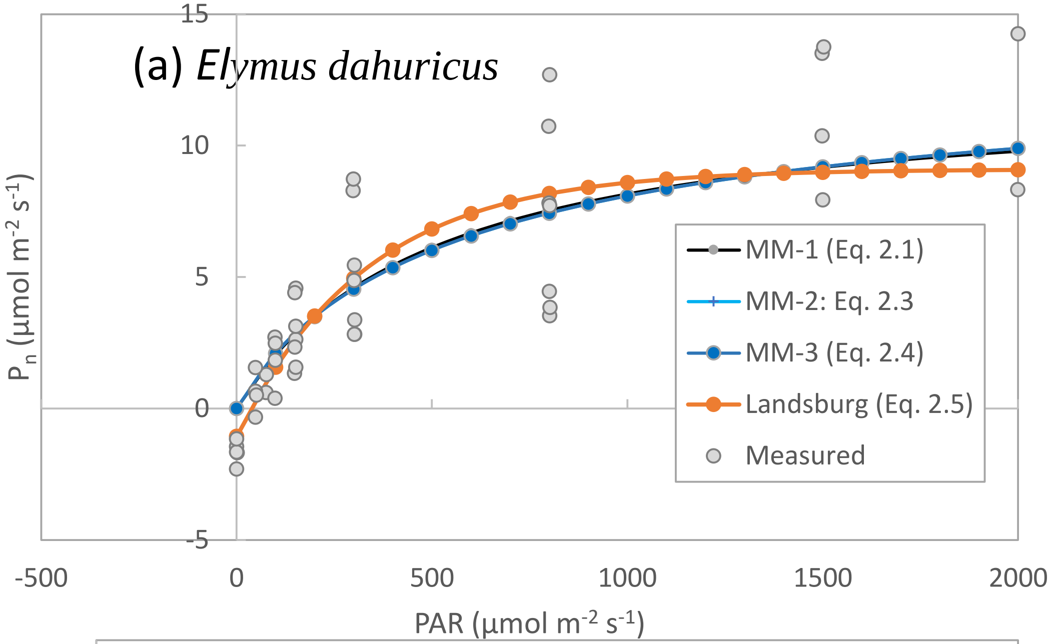
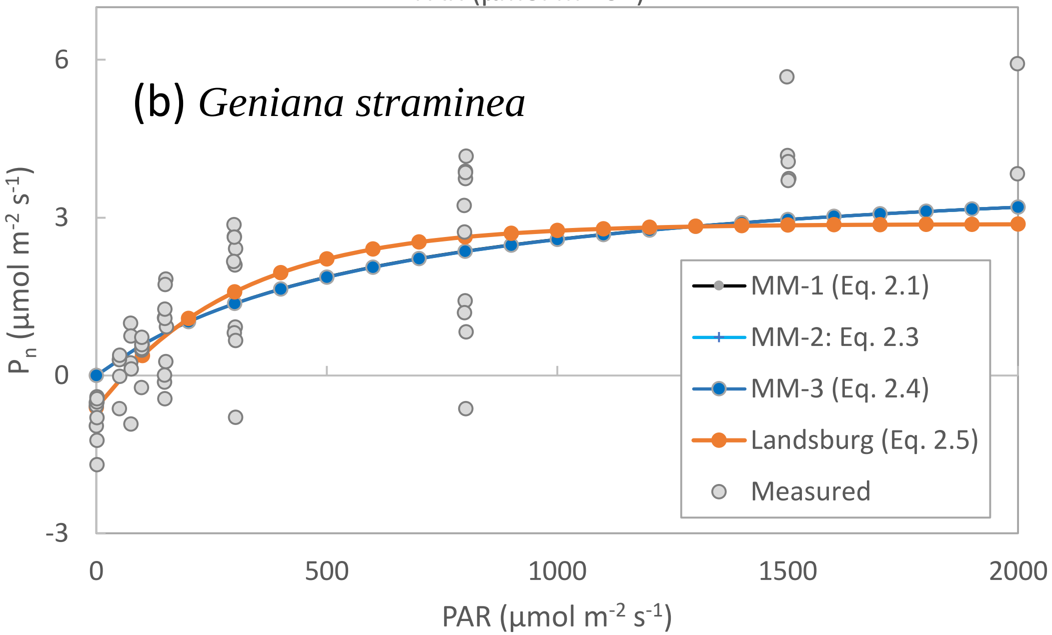


Figure 2-7. Fitted light response curves using three Michaelis-Menten (MM) equations (Eqs. 2.2, 2.3. and 2.4) and the Landsberg model (Eq. 2.5) for two species on the Tibetan Plateau (Wang *et al.* 2018). Details are included in the supplement spreadsheet LightR_models.xlsx (S2-4).



	MM-1	MM-2	MM-3	Landsberg
α	0.024	0.027	0.027	-0.003
β		-0.421	-0.421	9.102
I_{comp}				36.83
P_m	12.224	13.108	13.108	
r^2	0.667	0.668	0.668	0.664
MSE	6.844	6.841	6.841	6.785



	MM-1	MM-2	MM-3	Landsberg
α	0.007	0.007	0.007	-0.003
β		4.213	4.215	2.879
I_{comp}				58.207
P_m	4.189	-0.025	-0.026	
r^2	0.520	0.520	0.520	0.526
MSE	1.536	1.536	1.536	1.475

Figure 2-8. Changes in photosynthesis rate (A_n) of two species in Wang *et al.* (2018) based on Farquhar's model (Eq. 2.6) with the maximum rate of Rubisco (V_{max}) (a) and maximum rate of electron transport (J_{max}) (b). Differences between Rubisco-limited model (Eq. 2.7) and light-limited model (Eq. 2.11) are shown in (c).

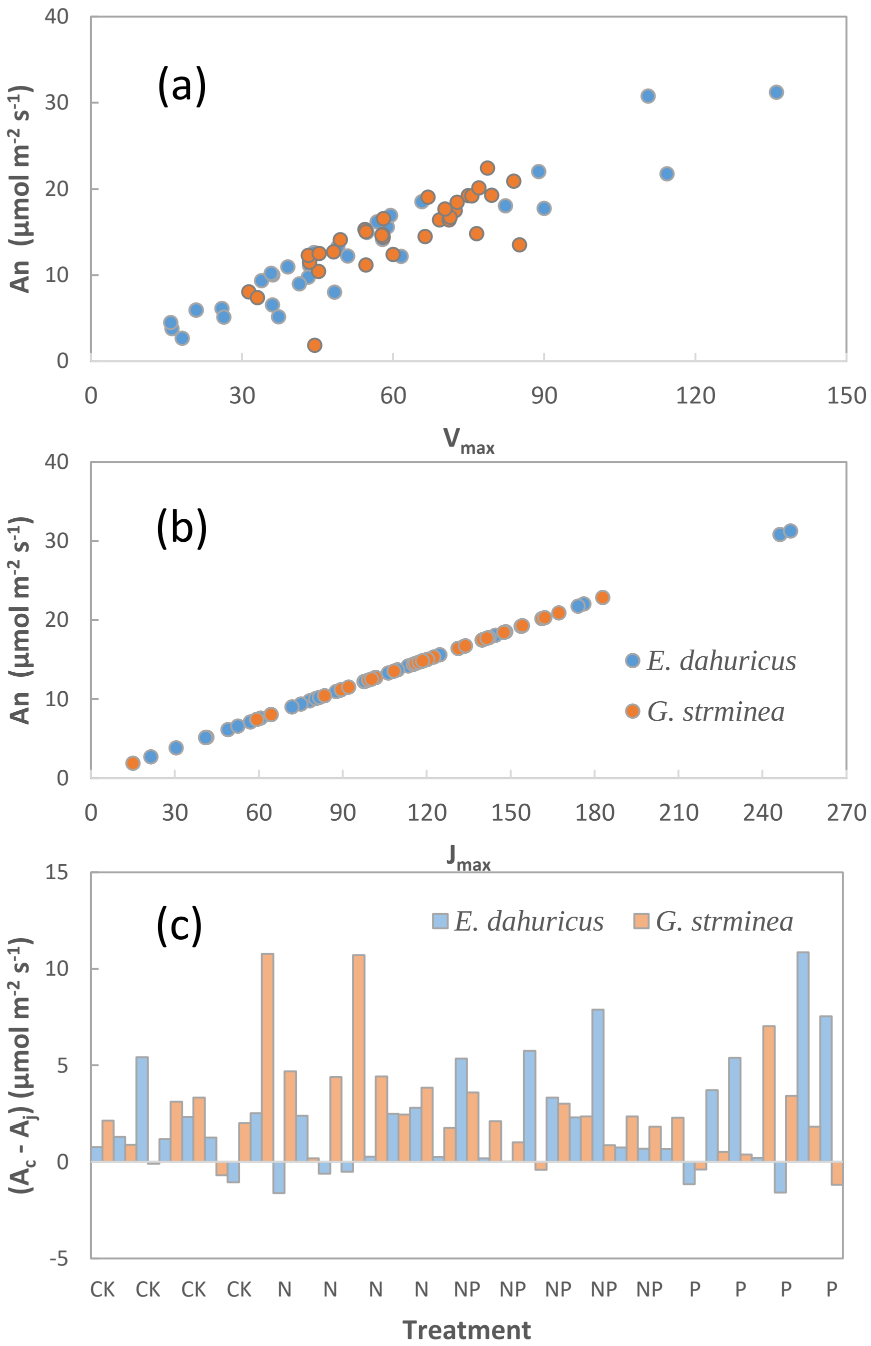
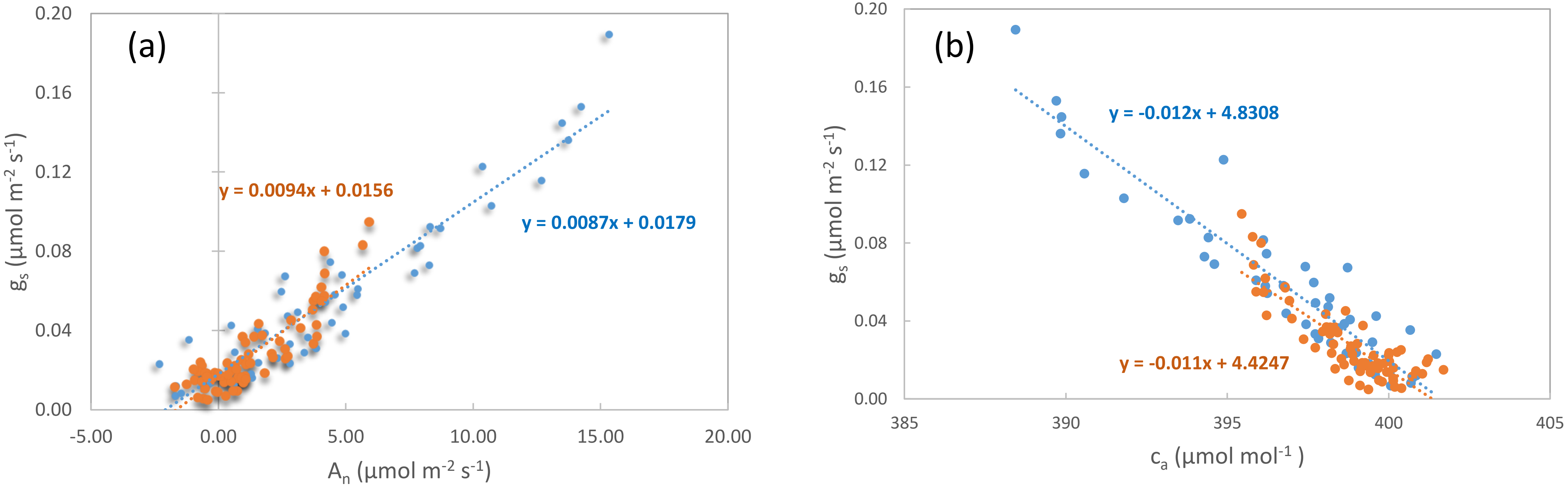


Figure 2-9. Changes in stomatal conductance (g_s) with photosynthesis rate (A_n) and leaf surface CO_2 concentration for two species studied in Wang *et al.* (2018). A_n was estimated with Farquhar's model (Eq. 2.6) and g_s was estimated with the Ball-Berry model (Eq. 2.15). The data and regression results are included in the supplement document S-3 (Wang2018.xlsx).



2.2.6 Light use efficiency (LUE) model
2.2.7 Nitrogen use efficiency (NUE) model
2.2.8 Water use efficiency (WUE) model

Scalars

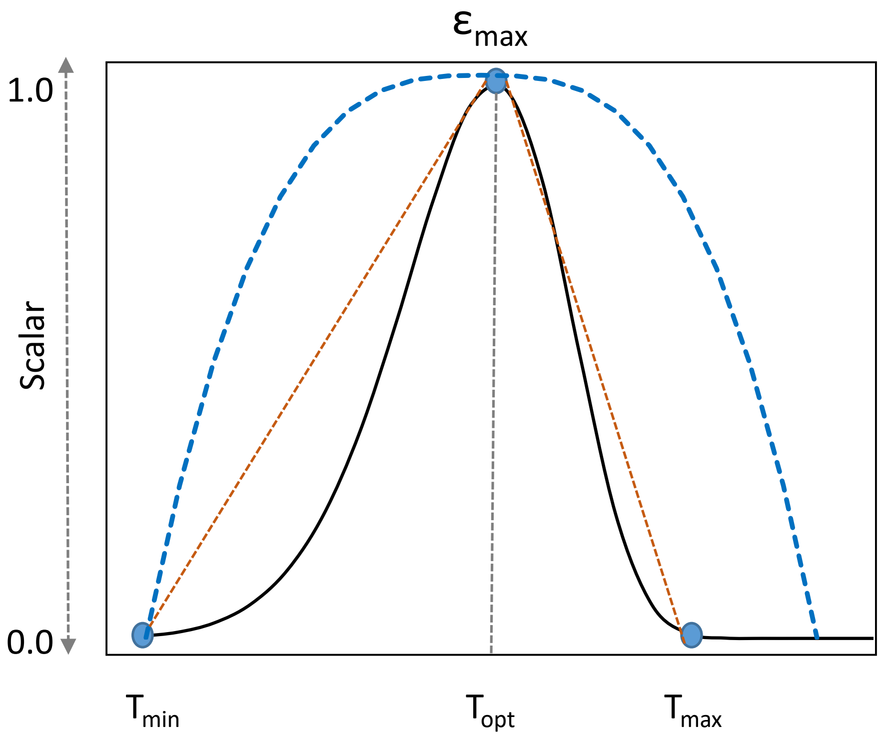
Ecosystem primary production (*GPP*, or *NPP*), or canopy photosynthesis (P_n), can be simply molded as a portion of *PAR* – light use efficiency (ε):

$$Pn = \varepsilon \cdot Water$$

LUE model for estimating ecosystem primary production is simple, using a*PAR* as the sole independent variable that is more available at ecosystem-regional-global scales. This advantage is the primary reason that the MODIS teams were able to measure global, continuous *GPP* based on Terra satellite data (Running *et al.* 2004). *GPP* is estimated as:

$$GPP = [\varepsilon_{max} \cdot \mathrm{mod}(\mathrm{Temperature}) \cdot \mathrm{mod}(VPD)] \cdot aPAR$$

Figure 2-5. Scalar development for modifying resource use efficiency (ε) from its maximum value (ε_{max}). Both symmetric and asymmetric functions can be used for estimating ε from ε_{max}. Maximum (T_{min}), maximum (T_{max}) and optimum (T_{opt}) temperature are used for deriving temperature scalar of three asymmetric approaches.



PnET model

P_{max} (μmol CO_2 m^{-2} s^{-1}) is calculated with a simple linear model based on a meta-analysis of prior publications:

$$P_{max} = \alpha + \beta \cdot N\%$$

P_n is further modified for suboptimal environmental conditions (see Section 2.2.6) as:

$$P_n = \propto \cdot P_{max} \cdot \Delta T \cdot \Delta W \cdot \Delta VPD$$

Water use efficiency (WUE)

Assuming CO_2 uptake and H_2O loss are coupled, *GPP* at ecosystem can be molded as:

$$GPP = WUE \cdot ET$$

Multiple resource use model (mRUE)

GPP = resource supply × proportion of resource supply × captured efficiency of resource use

When multiple RUEs are integrated, GPP can be modeled as:

$$GPP = (R_{avail1} \cdot R_{avail2} \cdots R_{availn})^{1/n} \cdot (RUE_1 \cdot RUE_2 \cdots RUE_n)^{1/n}$$

Summary

- Models based on light response curve are easy to understand and use. Only a few parameters (2-4) are needed to construct these models. Much more efforts are needed to examine the influences of other potential driving forces on model parameters.
- Physiological models have solid chemical and physical processes and theoretical foundations. Farquhar's model is based on the Kinetic energy concept of the Michaelis-Menten model as well as the chemical processes of photosynthesis, whereas the Ball-Berry family of models are rooted in the gas diffusion process and the corresponding properties of gases and physical conditions.
- A large number of parameters (5-10) are required for both Farquhar's model and the Ball-Berry models. These parameters are often difficult to measure or estimate. When these models are used to model ecosystem production, a tremendous amount of ancillary data on species composition, structure, soil conditions and microclimate are needed.
- Resource use models are also easy to understand and can be based on empirical parameters. They are particularly advantageous for modeling ecosystem production at landscape-region-global scales. These models have specific merits when applied with remote-sensed measures such as vegetation index, phenology, *etc.*

Supplementary Materials

S-1: Light response curves through Michaelis-Menten and Landsburg models (LightResponse.xlsx)

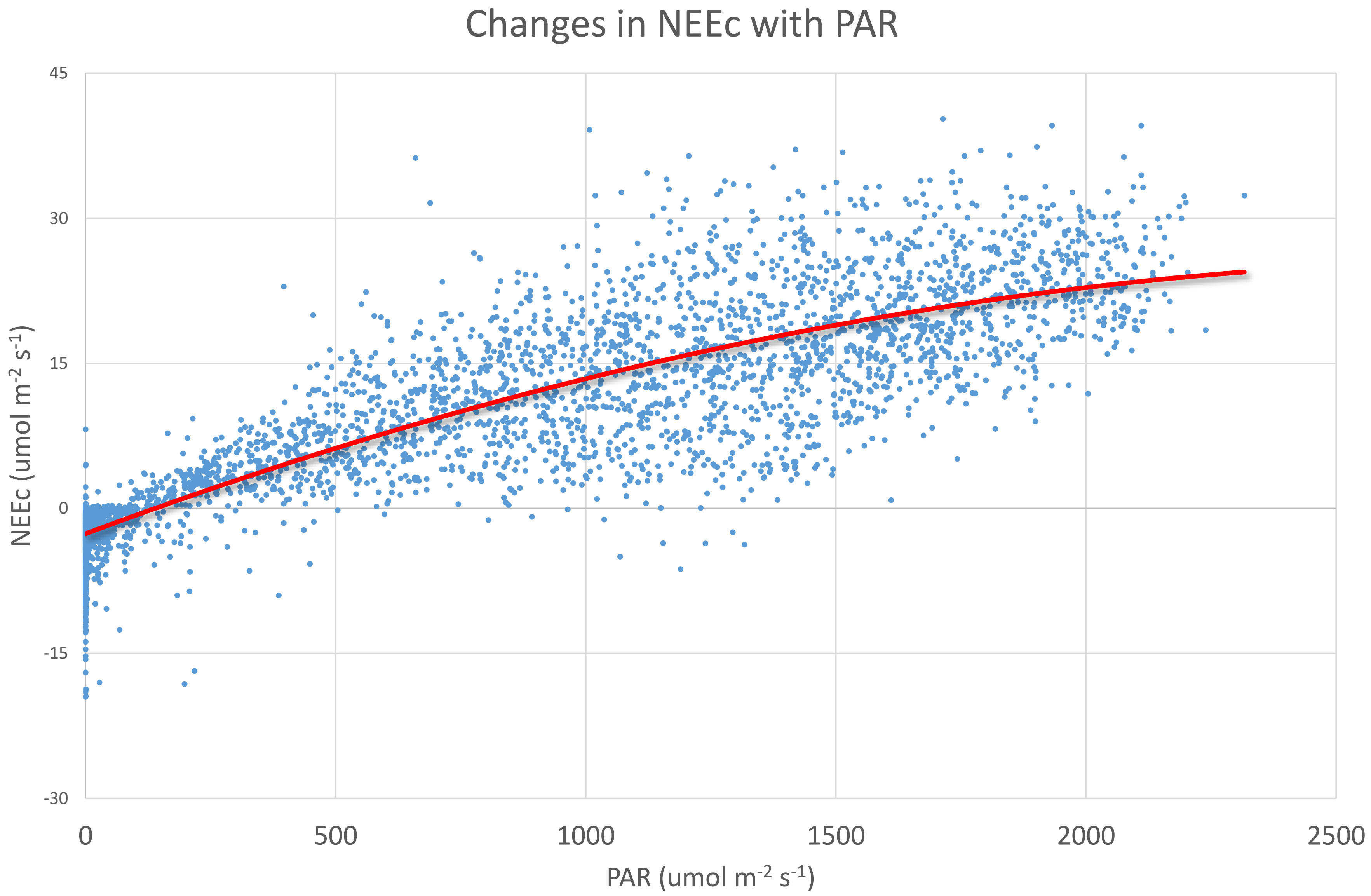
S-2: Simulations of stomatal conductance (g_s) based the Ball-Berry model (Ball_Berry_Model.xlsx)

S-3: Field measurements and modeled photosynthesis rate (A_n, μmol m^{-2} s^{-1}) and parameters for two species in Wang *et al.* (2018) (Wang2018.xlsx)

S-4: Model performances of Michaelis-Menten and Landsberg models for the two species in Wang et al. (2018) (LightR_models.xlsx)

S-5: Python codes for estimating empirical coefficients through nonlinear regression analysis of Michaelis-Menten models and Landsberg model (Chapter2_PY.RAR). This package has one dataset in Excel for practice and four Python programs for non-linear regression.

Homework 2


Changes in NEEc with PAR
45
30
15
0
-15
-30
NEEc (umol m-2 s-1)
0
500
1000
1500
2000
2500
PAR (umol m-2 s-1)

Homework 2:

In class exercise of MM and Landsberg models by group