

# Applications of Biophysical Models In Flux Studies

## GEO874-001: Climatic Changes, Impacts, and Biophysical Modeling

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**Course Information:** 3 credits; 9:00 – 12:00 a.m.; Tuesday; online for 2020

**Class Webpage:** <http://lees.geo.msu.edu/courses.html>

July 30, 2021  
Southwest University, Chongqing  
The 17<sup>th</sup> USCCC Annual Meeting

**Grading:** (1) Attendance – 10%; (2) Homework – 60%; (3) Term project – 30%

**Textbook:** Chen, J. 2021. Biophysical Models and Applications in Ecosystem Analysis. HEP/MSU Press.

China: <http://www.hep.com.cn/book/preview/details?uuid=683a89aa-175a-1000-92e7-b5ab40d78620>

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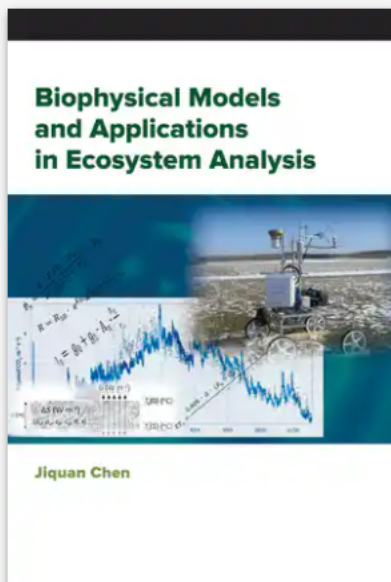
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# Order Information



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## Biophysical Models and Applications in Ecosystem Analysis

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By Jiquan Chen

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DESCRIPTION AUTHORS PRAISE

The past five decades have witnessed a rapid growth of computer models for simulating ecosystem functions and dynamics. This has been fueled by the availability of remote sensing data, computation capability, and cross-

**Course Description:** This graduate-level class is taught online or in person for student to understand the fundamental biophysical models in ecosystem analysis by focusing on the biophysical essentials, photosynthesis, respiration, evapotranspiration and global warming potentials. This class covers five major topics:

- Global climatic changes: causes, mechanism and consequences
- Scientific history, principles and evolvments of the models
- Biophysical models and applications in ecosystem studies
- Data sources, tools, analytical methods, and synthesis
- Hands on practices of key modules with real-world data and online demonstrations

# Ecosystem Models: What? Why?

- Abstractions of real-world system or process

60 Chapter 4

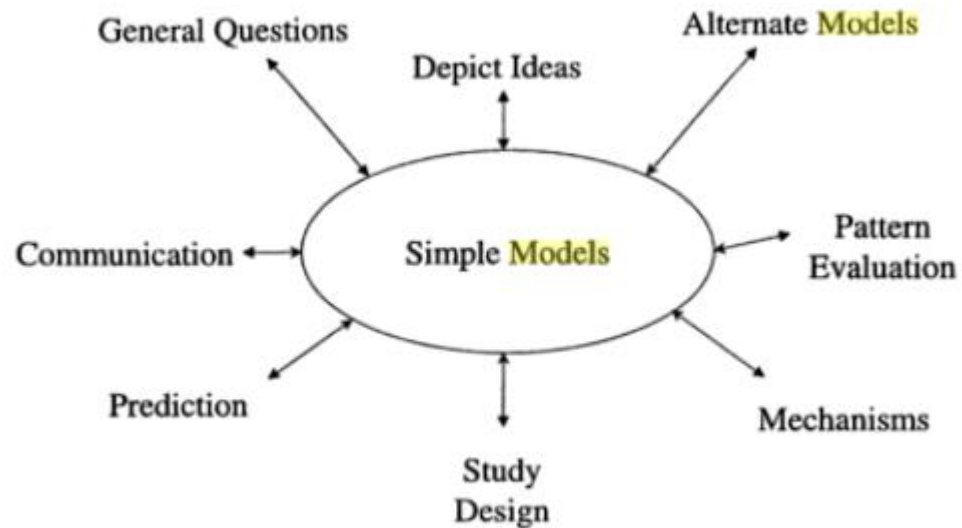


Figure 4.5. The utility of simple models in ecosystem science. The connections suggest that simple models can be effective tools toward progress in the various areas of research depicted.

Canham, C. D. W., Cole, J., & Lauenroth, W. K. (2003). *Models in ecosystem science*. Princeton University Press.

- 1) Explain (very distinct from predict)
- 2) Guide data collection
- 3) Illuminate core dynamics
- 4) Suggest dynamical analogies
- 5) Discover new questions
- 6) Promote a scientific habit of mind
- 7) Bound (bracket) outcomes to plausible ranges
- 8) Illuminate core uncertainties.
- 9) Offer crisis options in near-real time
- 10) Demonstrate tradeoffs / suggest efficiencies
- 11) Challenge the robustness of prevailing theory through perturbations
- 12) Expose prevailing wisdom as incompatible with available data
- 13) Train practitioners
- 14) Discipline the policy dialogue
- 15) Educate the general public
- 16) Reveal the apparently simple (complex) to be complex (simple)

Epstein, J. M. (2008). Why model?. *Journal of Artificial Societies and Social Simulation*, 11(4), 12.

# Pre-computer era models

- Look up tables
- Simple empirical relationships

## A tree

$$\text{Volume} = \alpha \cdot \text{DBH}^\beta$$

$$\text{Volume} = \alpha \cdot \text{Height} \cdot \text{DBH}^\beta$$

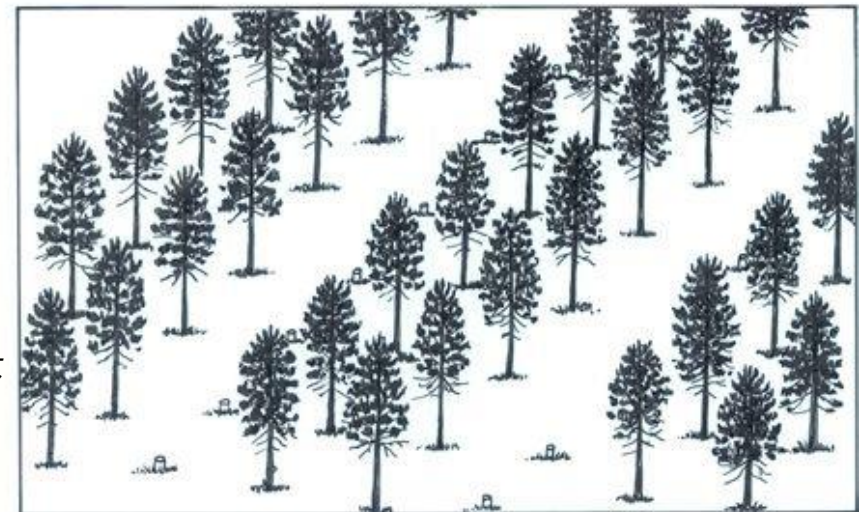
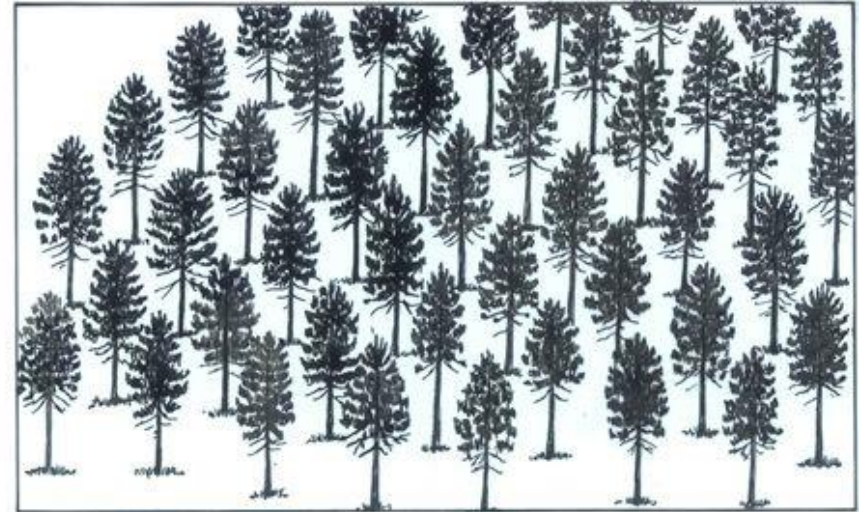
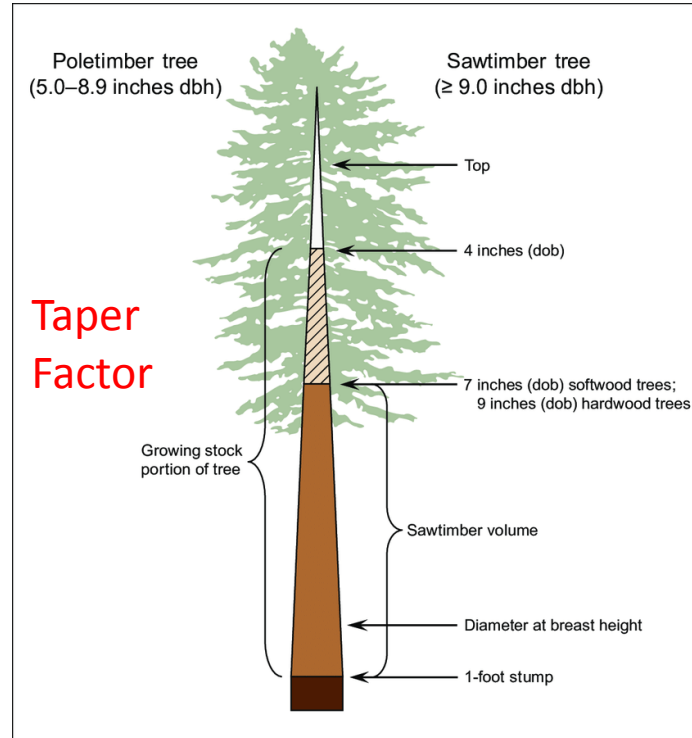
## A forest

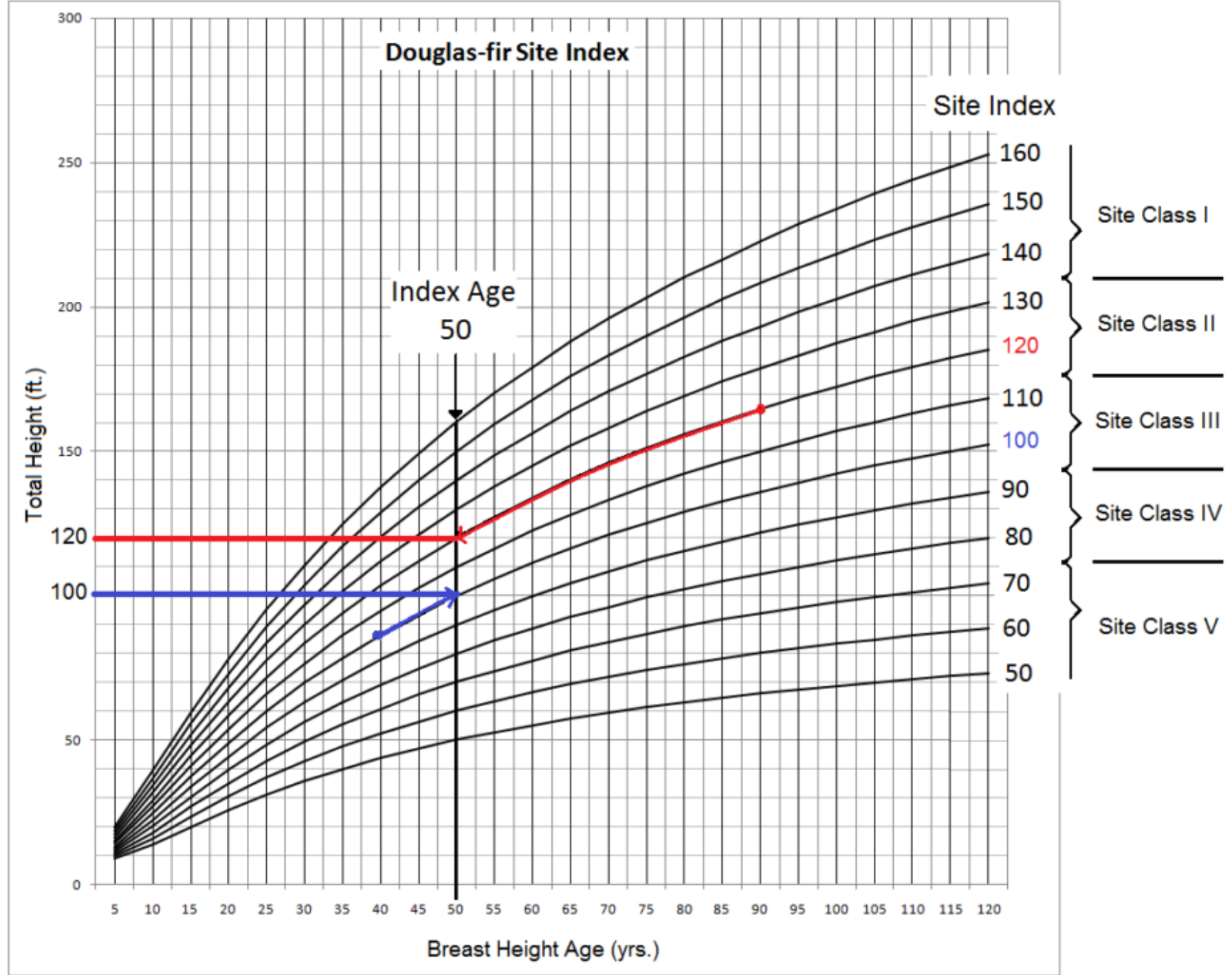
$$\text{Volume} = \alpha \cdot [\text{Height} \cdot \text{DBH}^\beta] \cdot \text{Density}$$

$$\text{Volume} = \alpha \cdot [\text{Height} \cdot \text{DBH}^\beta] \cdot \text{Density} \mid \text{Site Index} \mid \text{Species}$$

$$\text{Volume} = \alpha \cdot [\text{Height} \cdot \text{DBH}^\beta] \cdot \text{Density} \mid \text{Site Index} \mid \text{Species} \mid \text{management}$$

$$\text{Biomass} = \text{Volume} \cdot \text{Wood Density}$$

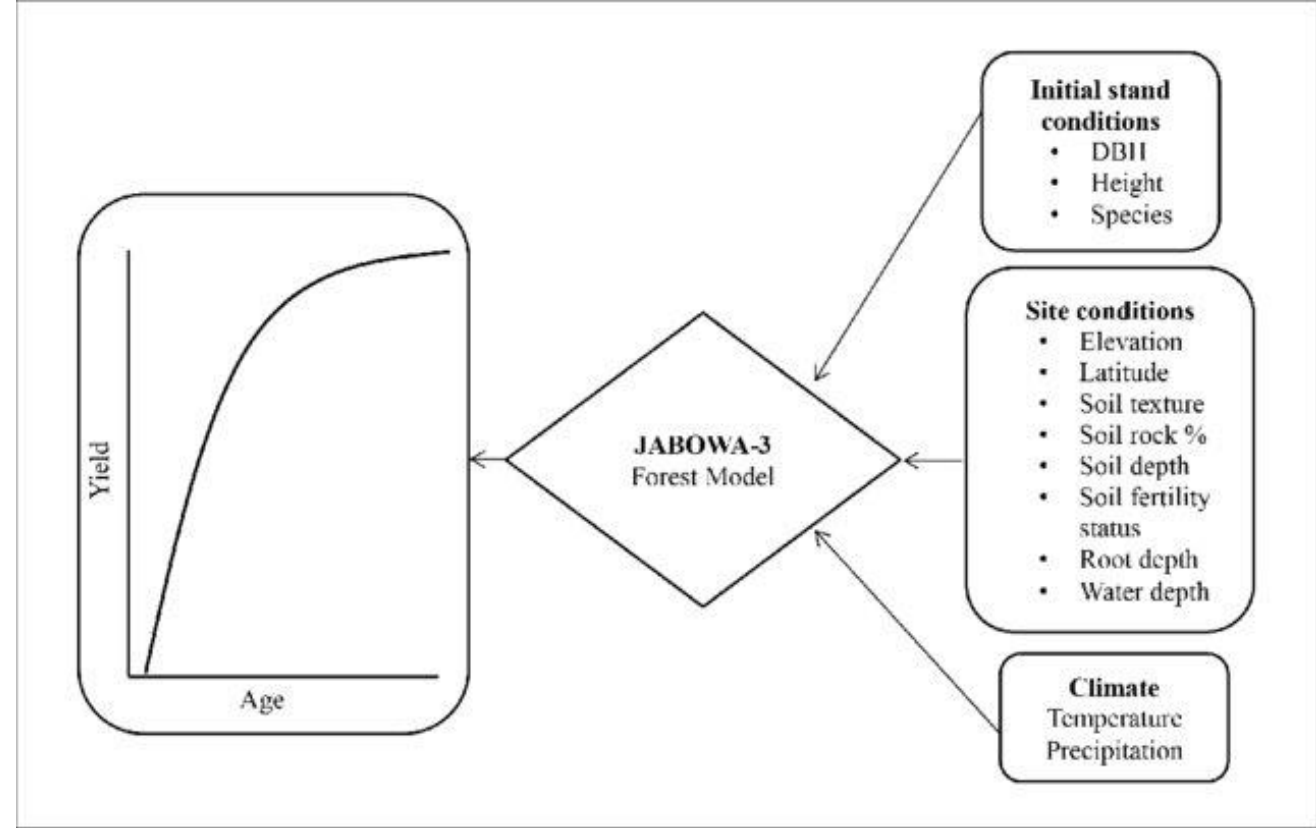






# Computer era models

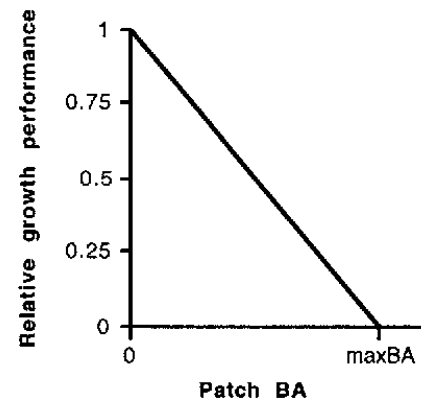
- Increasing the number of variables
- Mostly based on empirical relationships
- Climatic, soil, disturbances, management as regulators
- Interactions among components (e.g., species, soil-plants) are considered
- Example: JOBAWA, FORET models (a.k.a. GAP models)



Ashraf, M. I., Bourque, C. P. A., MacLean, D. A., Erdle, T., & Meng, F. R. (2012). Using JABOWA-3 for forest growth and yield predictions under diverse forest conditions of Nova Scotia, Canada. *The Forestry Chronicle*, 88(6), 708-721.

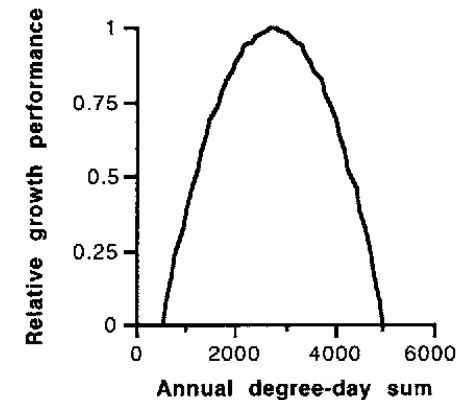
a)

**Crowding-dependent growth performance**



b)

**Temperature-dependent growth performance**



Individual-based models (IBMs) of complex systems emerged in the 1960s and early 1970s, across diverse disciplines from astronomy to zoology. Ecological IBMs arose with seemingly independent origins out of the tradition of understanding the ecosystems dynamics of ecosystems from a 'bottom-up' accounting of the interactions of the parts. Individual trees are principal among the parts of forests. Because these models are computationally demanding, they have prospered as the power of digital computers has increased exponentially over the decades following the 1970s.

Shugart, H. H., Wang, B., Fischer, R., Ma, J., Fang, J., Yan, X., ... & Armstrong, A. H. (2018). Gap models and their individual-based relatives in the assessment of the consequences of global change. *Environmental Research Letters*, 13(3), 033001.

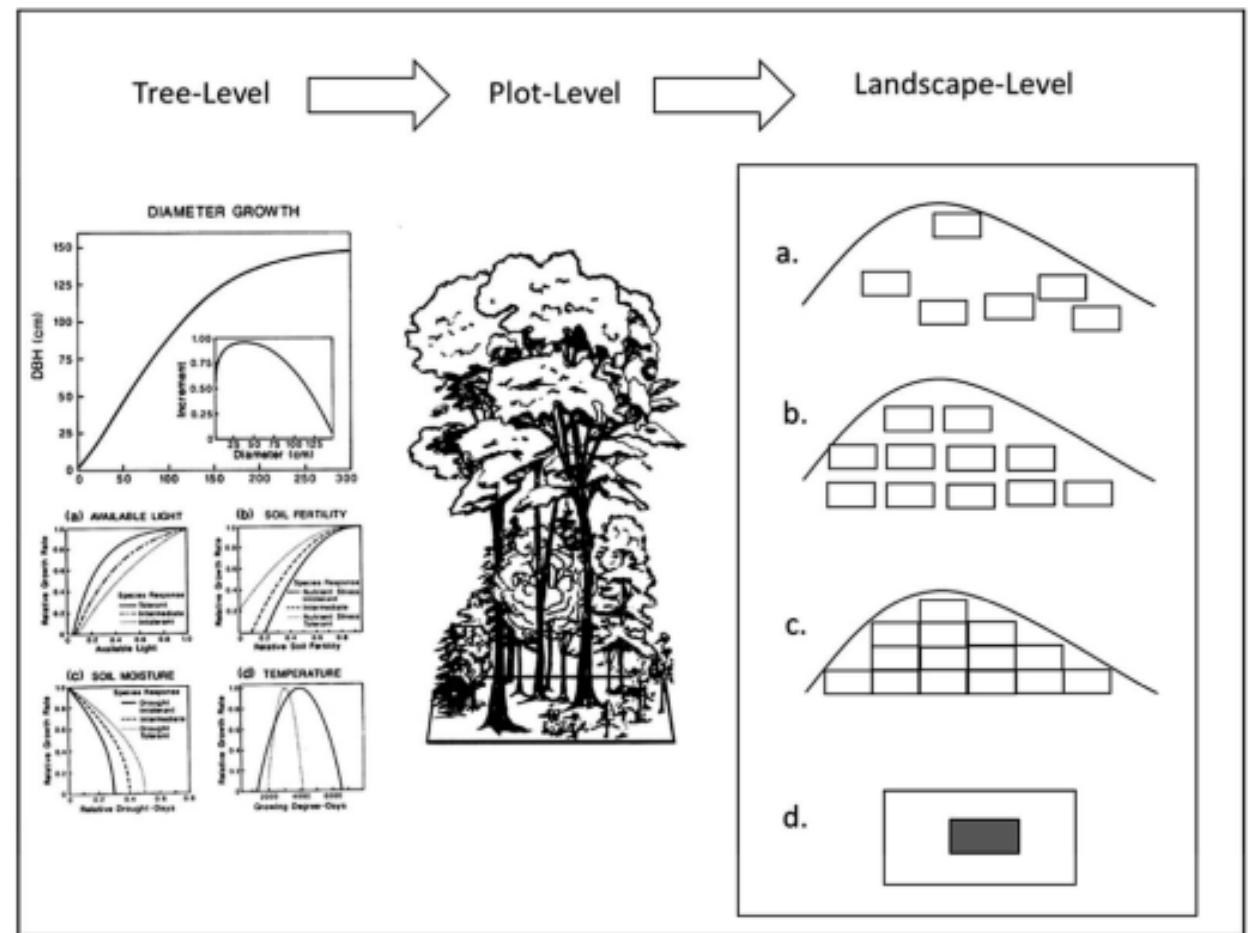
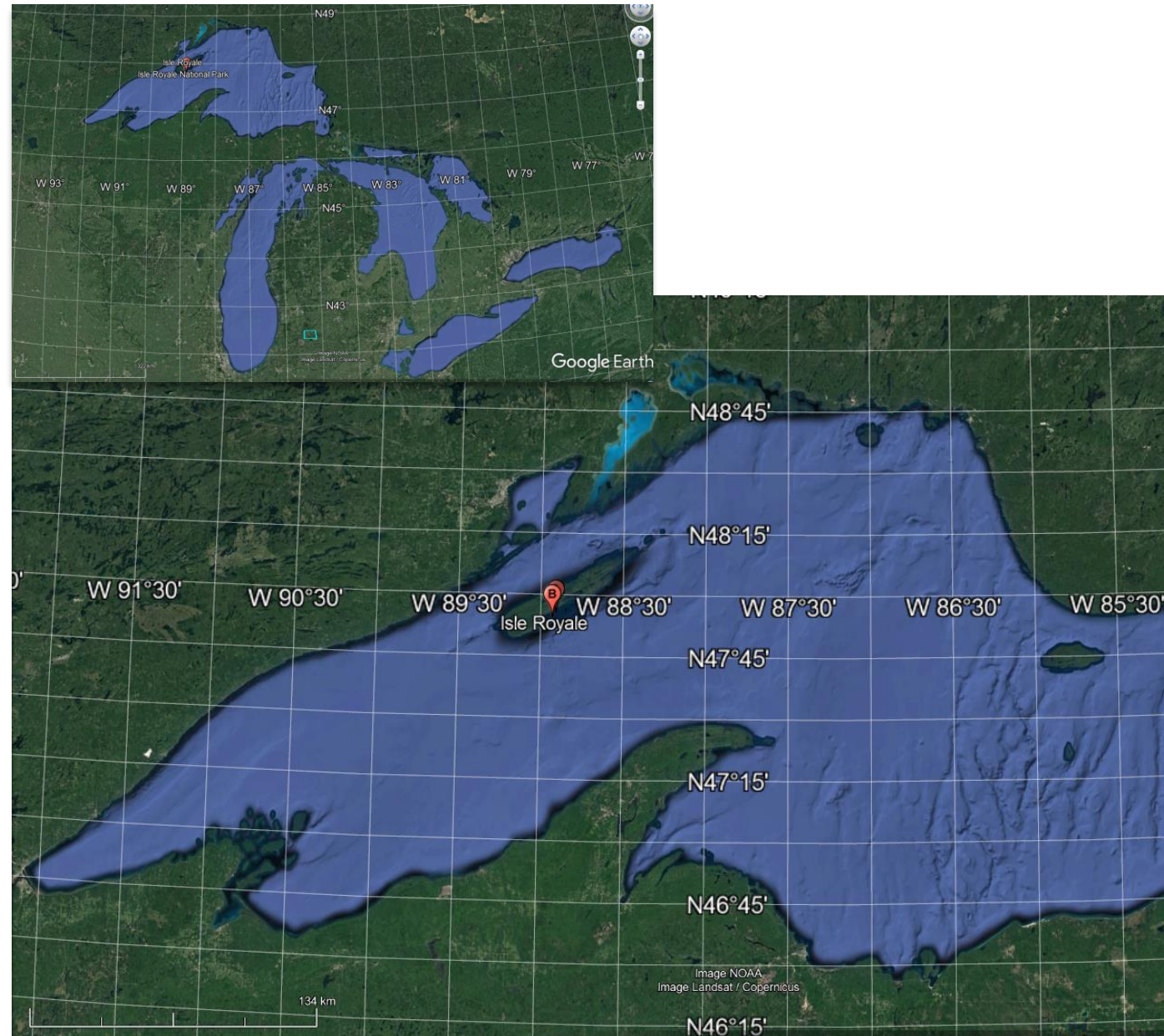
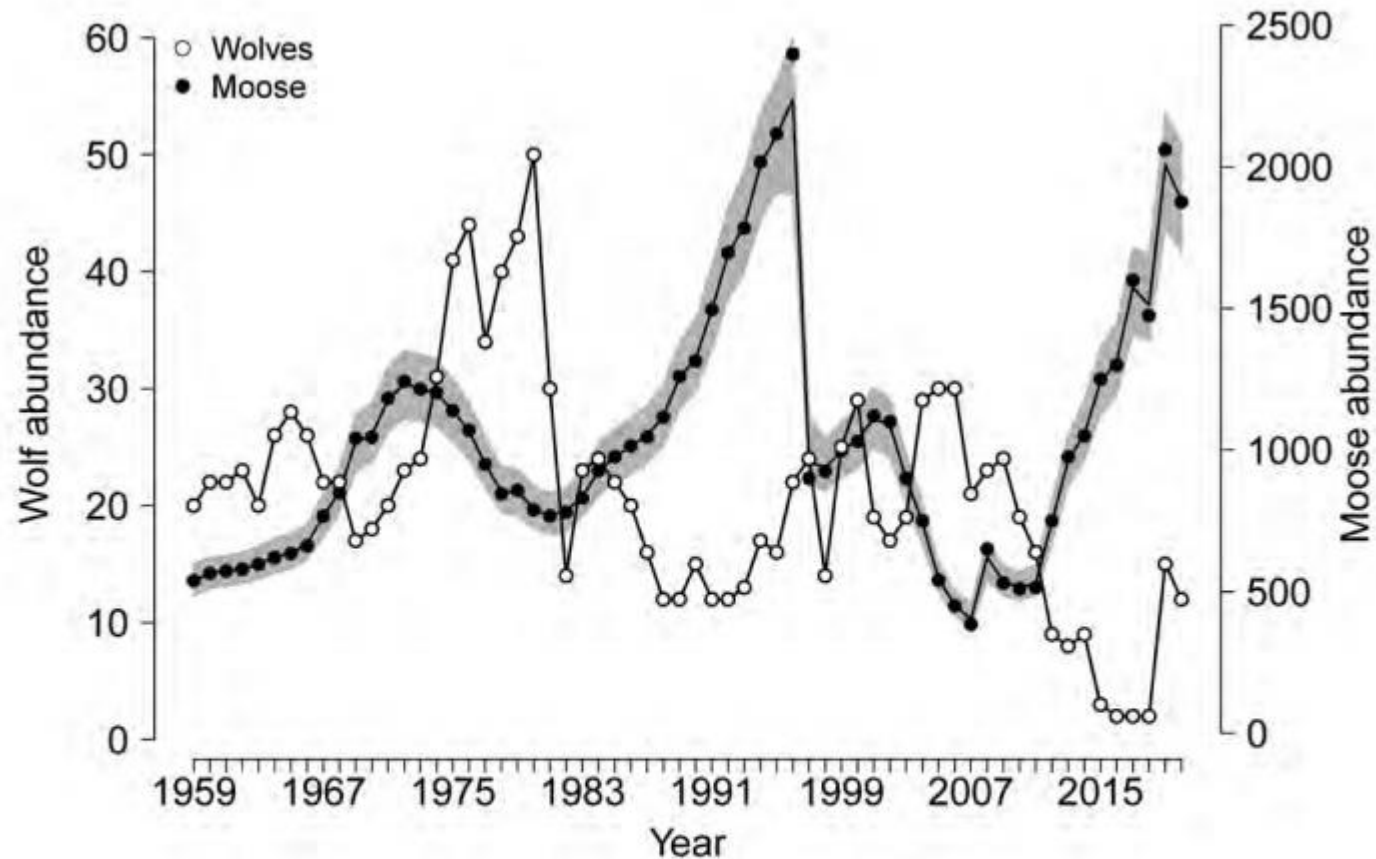


Figure 2. General functioning of a gap model. As one moves to the right to left, spatial scale increases from an individual tree to a small plot to a landscape. The tree-level response shown here is the elementary growth (or tree ring) equation from the FORET (Shugart and West 1977) model. The magnitude of the tree-mortality probability of each tree are also determined at the tree-level depending on tree growth as an index of vigor, species longevities and other conditions. The form of the growth equation with no constraints is shown at the top and the decrement to this optimal growth equation is found below according to the particular controlling environmental factors (available light, soil moisture, etc). At the plot level, the vertical profile of light, available soil moisture, and other environmental and biogeochemical factors are calculated and tree to tree interactions are computed. Conditions for potential new seedlings for each year are determined factors such as the environmental conditions and seed sources. At the landscape model, a basic gap model can be used to represent the landscape as: (a) the summation of a Monte Carlo collection of independent random points; (b) gridded points at some spacing, (c) a tessellation of adjacent plots; (d) a spatially explicit landscape simulation with a spatial map of trees that is 'windowed' or updated for tree birth, growth and death by dropping a gap-model computational window onto the tree-stem map to solve for a subset of a new map. This is repeated to produce the new map. The size of this subset determines the resolution of the spatial map.

# Population Dynamics: Predator-Prey Relationship (



# Population Dynamics: Predator-Prey Relationship (Wolf-Moose on Isle Royal National Park)



## The BIDE Model

$$\text{Population} = \begin{aligned} &+ \text{Birth} \\ &+ \text{Immigration} \\ &+ \text{Death} \\ &+ \text{Emigration} \end{aligned}$$

Death = function (Wolf Population)

**Figure 1.** Wolf and moose fluctuations in Isle Royale National Park, 1959-2020. Wolf abundances (open circles) were based on aerial surveys conducted from January to March. The sudden increase in wolf abundance in 2019 is the result of wolves being translocated by the National Park Service. Moose abundances (filled circles) during 1959-2001 are based on population reconstruction from the recoveries of dead moose, and estimates from 2002 to 2020 are based on aerial surveys. The second set of moose abundances (lines) and confidence intervals (shaded area) are results of a Bayesian state-space model that takes account of density dependence and age structure, as well as sampling error (Hoy et al. 2020, Functional Ecology). By contrast, confidence intervals reported in the main text emphasize sampling error associated with aerial surveys.

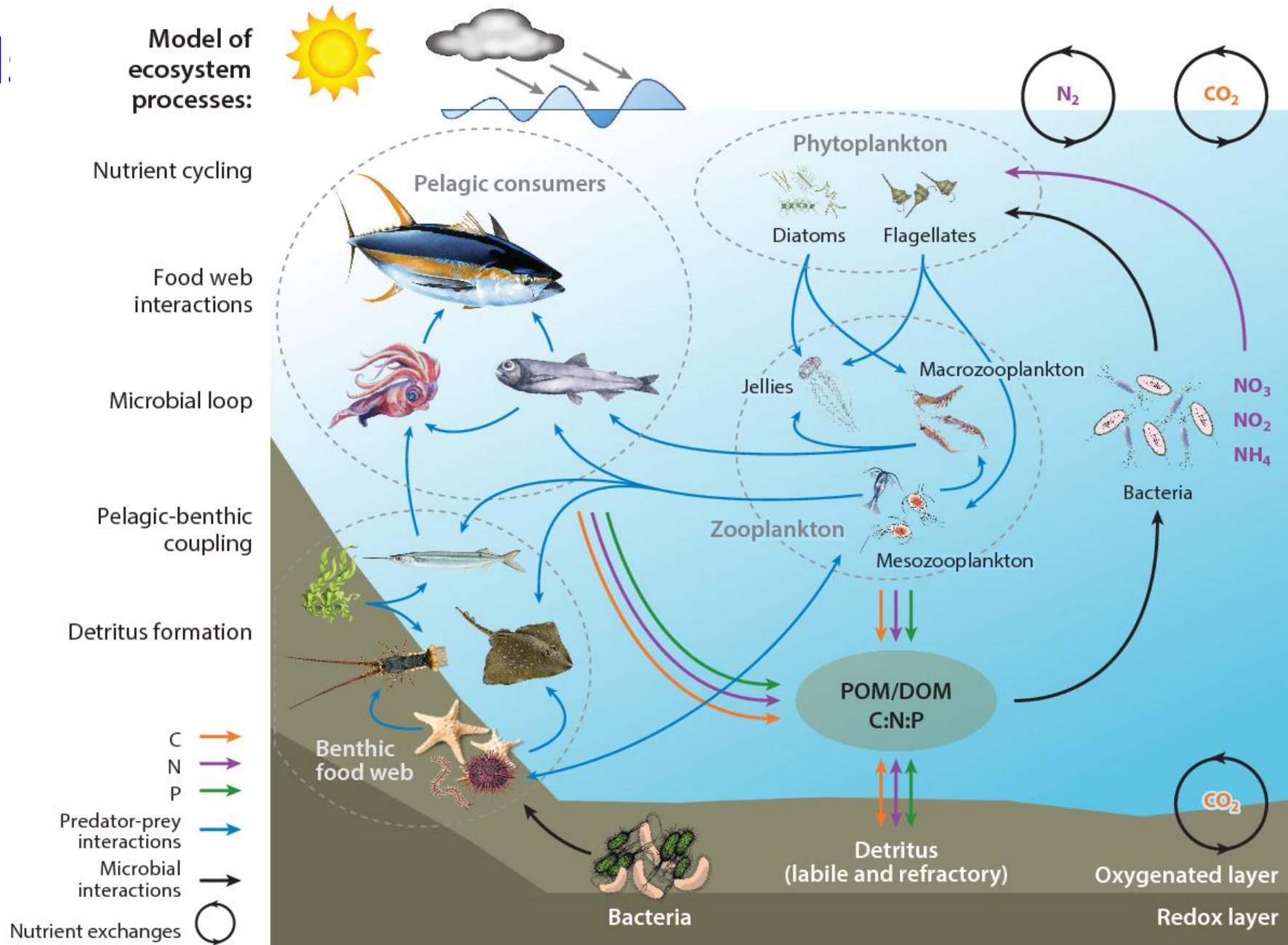
<https://www.youtube.com/watch?v=PdwnfPurXcs>

# Ecosystem Model:

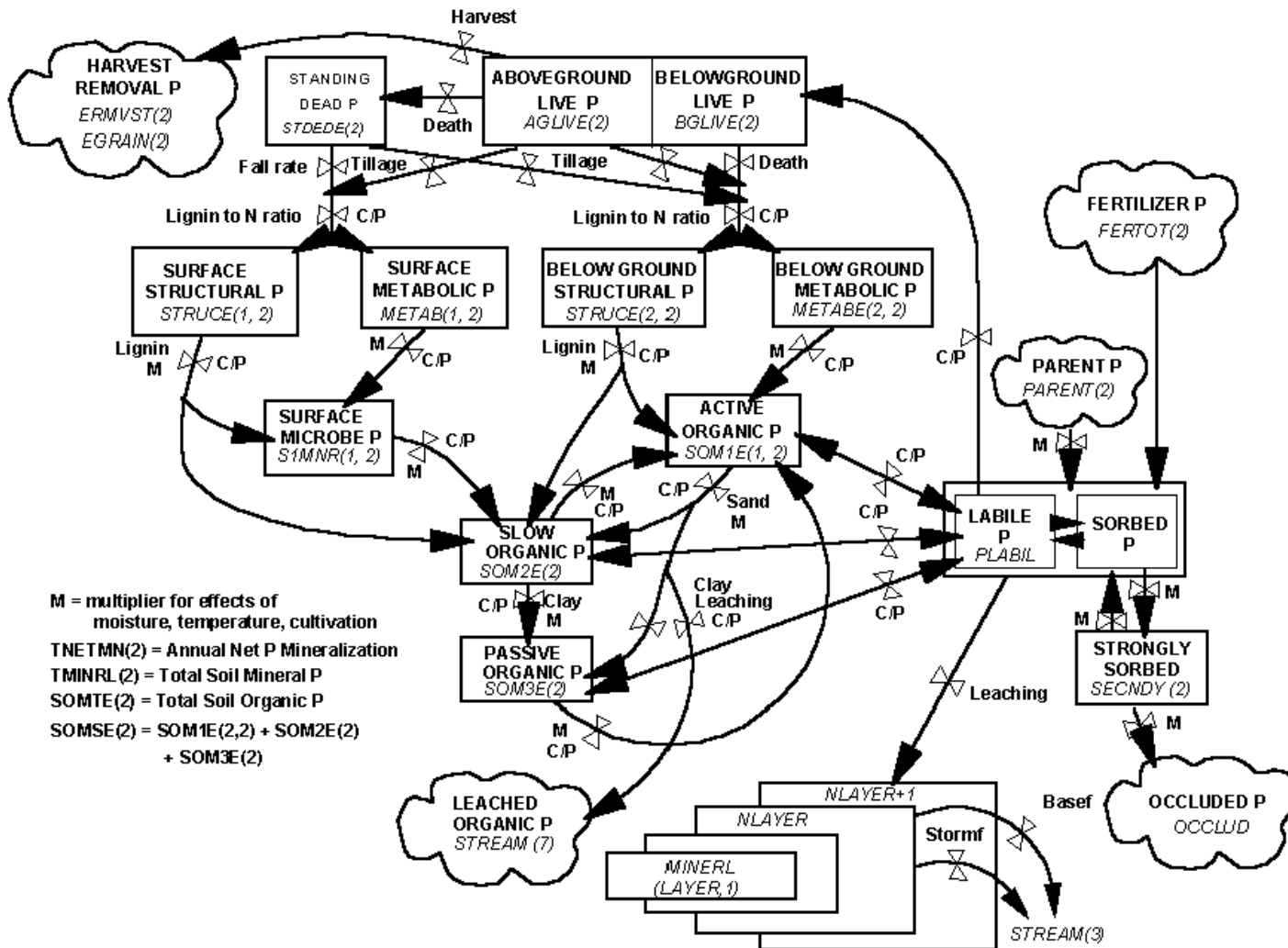
flows of mass and energy through an ecosystems

Fluxes among the components expressed as differential equations!

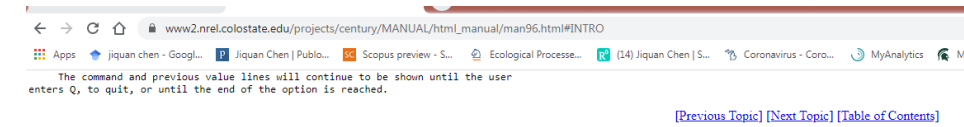
Pethybridge, H. R., Choy, C. A., Polovina, J. J., & Fulton, E. A. (2018). Improving marine ecosystem models with biochemical tracers. *Annual review of marine science*, 10, 199-228.



# Ecosystem Models: more examples



## Open Source Codes



### 4.5. Changing an Option

The user may change values of parameters within an existing option. After entering 2, for changing, the program will display each option which exists in the file and ask if the user would like to change that option:

```
Current option is N1 Wheat-type-one
Is this an option you wish to change
```

A response of "Y" or "y" will cause the program to move on to the change phase. If no option is responded to with a yes answer, the program will return to the previous menu of five actions. Once an affirmative response has been given, the user will be asked for a new abbreviation and description:

```
Enter a new abbreviation or a <return>
```

```
to use the existing abbreviation:
```

A new abbreviation must be unique to that file and no more than 5 characters; if a duplicate is entered, the user will be asked to enter another abbreviation.

```
Enter a new description or a <return>
```

```
to use the existing description:
```

The description may not be longer than 65 characters. Then, for each value in that option, the program will display the existing value for that parameter and ask the user for a new value:

```
Commands: D F H L Q <new value> <return>
```

```
Name: PRDX(1) Previous value: 300
```

```
Enter response:
```

The user may enter any of these possible responses, as shown on the Command line:

```
see the definition of that parameter ..... enter D
find a specific parameter in that option ..... enter F
see a help message ..... enter H
list the next 12 parameters ..... enter L
quit, retaining the old values for
this and the remaining parameters
in this option ..... enter Q
take the old value ..... enter <return>
enter a new value ..... enter a new value
```

The command and previous value lines will continue to be shown until the user enters Q, to quit, or until the end of the file is reached. Finally, the user is asked if changes made should be saved:

```
Do you want to save the changes made?
```

If this is answered with "Y" or "y", the changed values will be saved. Otherwise, the changes will be lost.

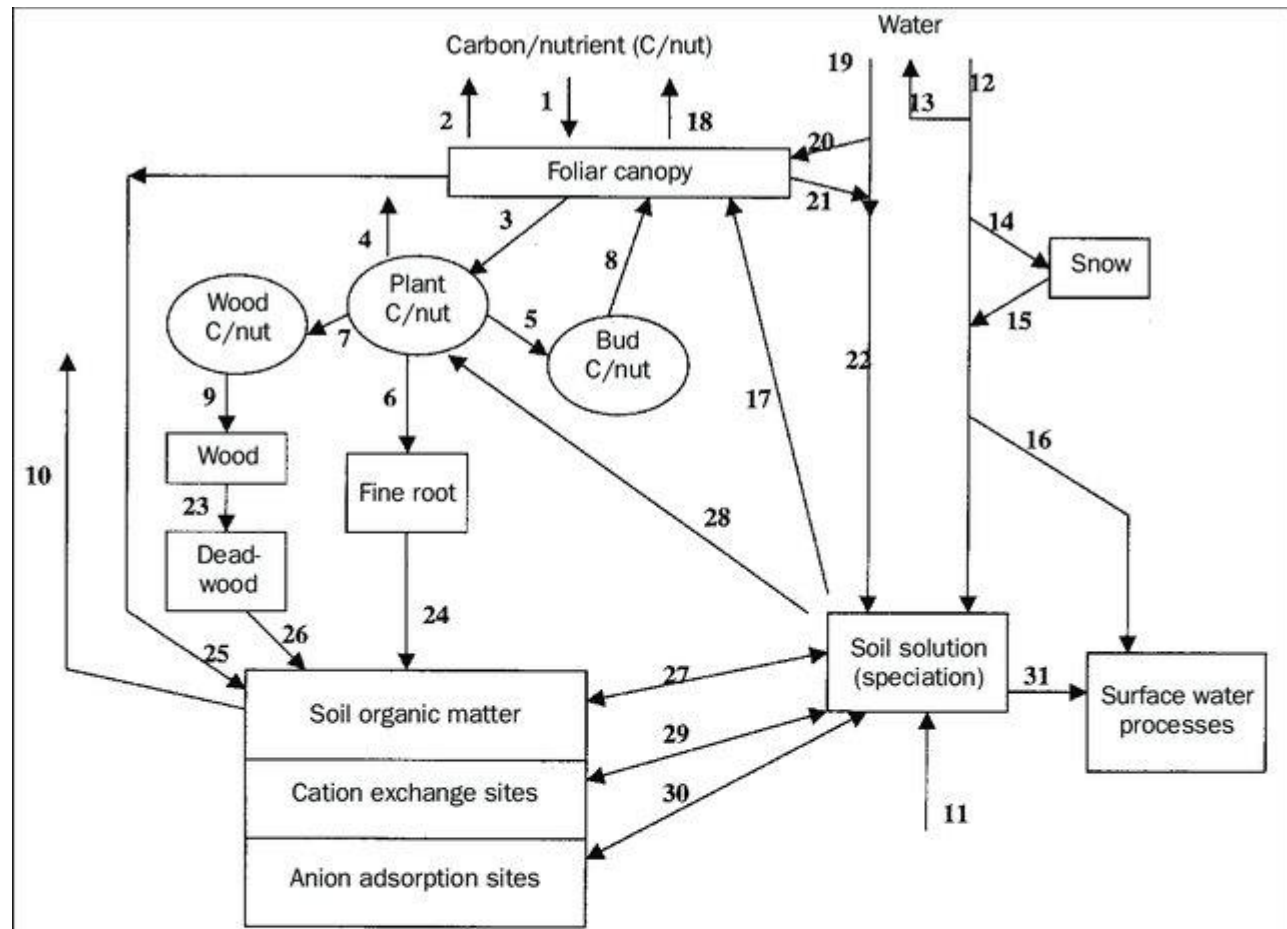
[\[Previous Topic\]](#) [\[Next Topic\]](#) [\[Table of Contents\]](#)

### 4.6. Changing the <site>-100 File

**PnET** is a suite of three nested computer **models** which provide a modular approach to simulating the carbon, water and nitrogen dynamics of forest **ecosystems**.

([https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds\\_id=817](https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=817))

Aber, J.D., S.V. Ollinger, C.T. Driscoll, C.A. Federer, and P.B. Reich. 2005. PnET Models: Carbon, Nitrogen, Water Dynamics in Forest Ecosystems (Vers. 4 and 5). ORNL DAAC, Oak Ridge, Tennessee, USA. <https://doi.org/10.3334/ORNLDAAC/817>



Processes depicted:

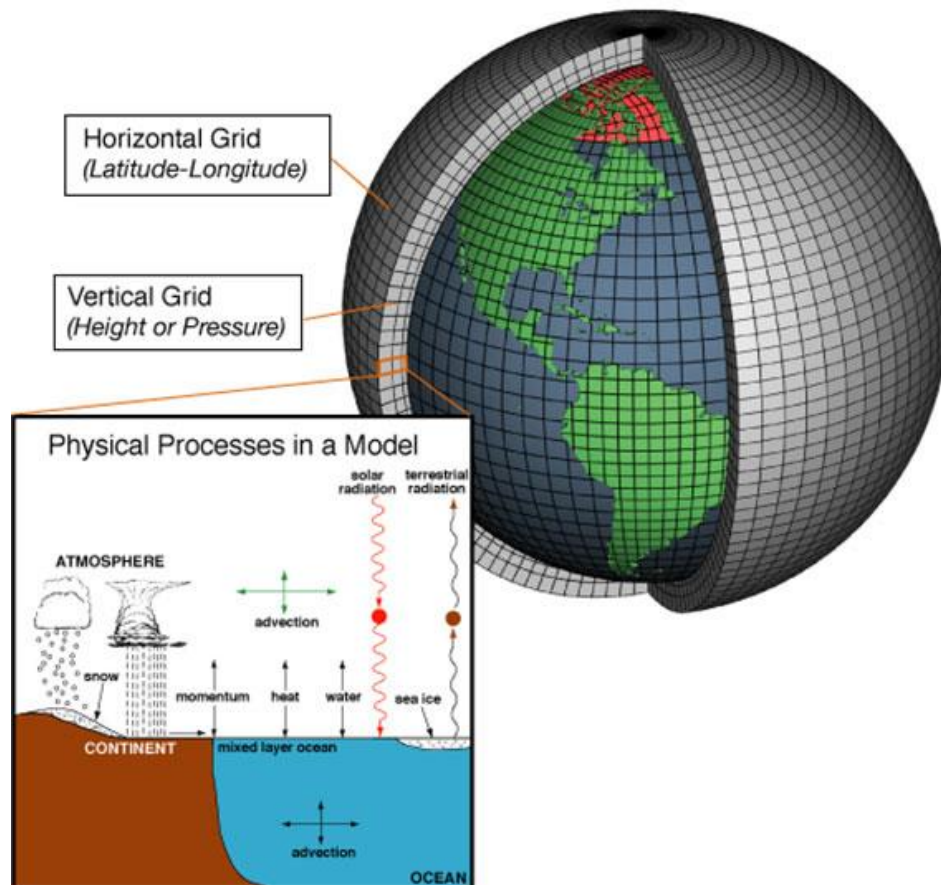
- |                                       |                                   |
|---------------------------------------|-----------------------------------|
| 1. Gross photosynthesis               | 16. Shallow flow                  |
| 2. Foliar respiration                 | 17. Water uptake                  |
| 3. Transfer to mobile carbon          | 18. Transpiration                 |
| 4. Growth and maintenance respiration | 19. Deposition (wet and dry)      |
| 5. Allocation to buds                 | 20. Foliar nutrient uptake        |
| 6. Allocation to fine roots           | 21. Foliar exudation              |
| 7. Allocation to wood                 | 22. Throughfall and stemflow      |
| 8. Foliar production                  | 23. Wood litter                   |
| 9. Wood production                    | 24. Root litter                   |
| 10. Soil respiration                  | 25. Foliar litter                 |
| 11. Weathering supply                 | 26. Wood decay                    |
| 12. Precipitation                     | 27. Mineralization/immobilization |
| 13. Interception                      | 28. Nutrient uptake               |
| 14. Snow-rain partition               | 29. Cation exchange reactions     |
| 15. Snowmelt                          | 30. Anion adsorption reactions    |
|                                       | 31. Drainage                      |

[https://www.researchgate.net/publication/232688300\\_Nor\\_Gloom\\_of\\_Night\\_A\\_New\\_Conceptual\\_Model\\_for\\_the\\_Hubbard\\_Brook\\_Ecosystem\\_Study/figures?lo=1](https://www.researchgate.net/publication/232688300_Nor_Gloom_of_Night_A_New_Conceptual_Model_for_the_Hubbard_Brook_Ecosystem_Study/figures?lo=1)

## What is an Earth System Model (ESM)?

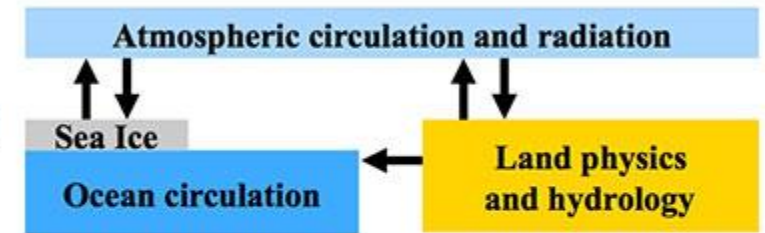
A coupled climate model is a computer code that estimates the solution to differential equations of fluid motion and thermodynamics to obtain time and space dependent values for temperature, winds and currents, moisture and/or salinity and pressure in the atmosphere and ocean. Components of a climate model simulate the atmosphere, the ocean, sea, ice, the land surface and the vegetation on land and the biogeochemistry of the ocean.

<https://soccom.princeton.edu/content/what-earth-system-model-esm>

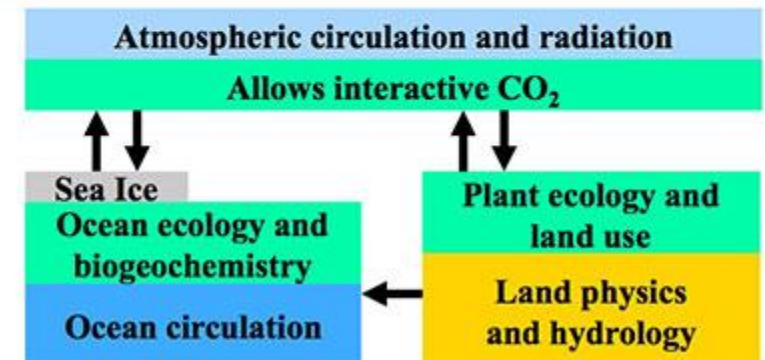


### An Earth System Model (ESM) closes the carbon cycle

**Climate Model**



**Earth System Model**





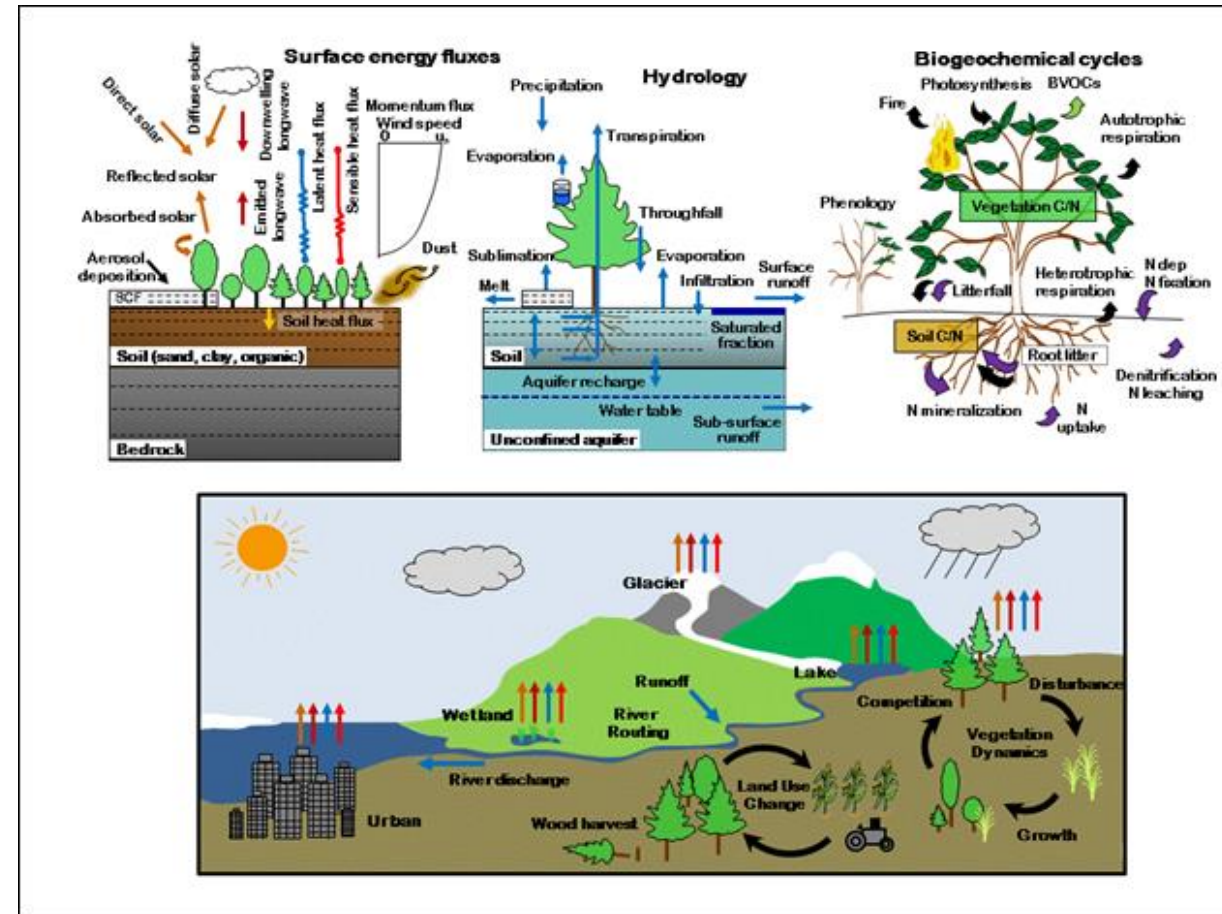
**COMMUNITY LAND MODEL (CLM)**: the land model for the [Community Earth System Model \(CESM\)](http://www.cesm.ucar.edu/models/cesm1/land/).

The model represents several aspects of the land surface including [surface heterogeneity](#) and consists of components or submodels related to [land biogeophysics](#), the [hydrologic cycle](#), [biogeochemistry](#), [human dimensions](#), and [ecosystem dynamics](#). Specific processes that are represented include:

- Vegetation composition, structure, and phenology
- Absorption, reflection, and transmittance of solar radiation
- Absorption and emission of longwave radiation
- Momentum, sensible heat (ground and canopy), and latent heat (ground evaporation, canopy evaporation, transpiration) fluxes
- Heat transfer in soil and snow including phase change
- Canopy hydrology (interception, throughfall, and drip)
- Snow hydrology (snow accumulation and melt, compaction, water transfer between snow layers)
- Soil hydrology (surface runoff, infiltration, redistribution of water within the column, sub-surface drainage, groundwater)
- Plant hydrodynamics
- Stomatal physiology and photosynthesis
- Lake temperatures and fluxes
- Dust deposition and fluxes
- Routing of runoff from rivers to ocean
- Volatile organic compounds emissions
- Urban energy balance and climate
- Carbon-nitrogen cycling
- Dynamic landcover change
- Land management including crops and crop management and wood harvest
- Ecosystem Demography (FATES, optional)

# Need a supercomputer to run!

<http://www.cesm.ucar.edu/models/clm/>



Schaefer, K., Schwalm, C. R., Williams, C., Arain, M. A., Barr, A., Chen, J. M., ... & Humphreys, E. (2012). A model-data comparison of gross primary productivity: Results from the North American Carbon Program site synthesis. *Journal of Geophysical Research: Biogeosciences*, 117(G3).

**Table 2.** Summary of Model Characteristics

Model	Number Sites	Time Step	Soil Layers <sup>a</sup>	Phenology <sup>b</sup>	Nitrogen Cycle	GPP Model <sup>c</sup>	Leaf-to-Canopy	Reference
AgroIBIS	5	Hourly	11	Prognostic	Yes	EK	Big-Leaf	<i>Kucharik and Twine [2007]</i>
BEPS	10	Daily	3	Semi-prognostic	Yes	EK	2-Leaf	<i>Liu et al. [1999]</i>
Biome-BGC	33	Daily	1	Prognostic	Yes	EK	2-Leaf	<i>Thornton et al. [2005]</i>
Can-IBIS	24	Hourly	7	Prognostic	Yes	EK	2-Leaf	<i>Liu et al. [2005]</i>
CN-CLASS	28	Hourly	3	Prognostic	Yes	EK	2-Leaf	<i>Arain et al. [2006]</i>
DLEM	30	Daily	2	Semi-prognostic	Yes	EK	2-Leaf	<i>Tian et al. [2010]</i>
DNDC	5	Daily	10	Prognostic	Yes	LUE	Big-Leaf	<i>Li et al. [2010]</i>
Ecosys	35	Hourly	15	Prognostic	Yes	EK	2-Leaf	<i>Grant et al. [2009]</i>
ED2	24	Hourly	9	Prognostic	Yes	EK	2-Leaf	<i>Medvigy et al. [2009]</i>
EDCM	9	Daily	10	Prognostic	Yes	LUE	Big-Leaf	<i>Liu et al. [2003]</i>
ISAM	13	Hourly	10	Prognostic	Yes	LUE	2-Leaf	<i>Yang et al. [2009]</i>
ISOLSM	9	Hourly	20	Observed	No	EK	2-Leaf	<i>Riley et al. [2002]</i>
LoTEC	10	Hourly	14	Prognostic	No	EK	Big-Leaf	<i>Hanson et al. [2004]</i>
LPJ	26	Daily	2	Prognostic	No	EK	Big-Leaf	<i>Sitch et al. [2003]</i>
MODIS_5.0	38	Daily	0	Observed	No	LUE	Big-Leaf	<i>Heinsch et al. [2003]</i>
MODIS_5.1	37	Daily	0	Observed	No	LUE	Big-Leaf	<i>Heinsch et al. [2003]</i>
MODIS_alg	39	Daily	0	Observed	No	LUE	Big-Leaf	<i>Heinsch et al. [2003]</i>
ORCHIDEE	32	Hourly	2	Prognostic	No	EK	Big-Leaf	<i>Krinner et al. [2005]</i>
SiB3	28	Hourly	10	Observed	No	EK	Big-Leaf	<i>Baker et al. [2008]</i>
SiBCASA	32	Hourly	25	Semi-prognostic	No	EK	Big-Leaf	<i>Schaefer et al. [2009]</i>
SiBcrop	5	Hourly	10	Prognostic	Yes	EK	Big-Leaf	<i>Lokupitiya et al. [2009]</i>
SSiB2	39	Hourly	3	Observed	No	EK	Big-Leaf	<i>Zhan et al. [2003]</i>
TECO	32	Hourly	10	Prognostic	No	EK	2-Leaf	<i>Weng and Luo [2008]</i>
TRIPLEX	6	Daily	0	Observed	Yes	LUE	Big-Leaf	<i>Peng et al. [2002]</i>

<sup>a</sup>Zero soil layers indicate the model does not have a prognostic submodel for soil temperature and moisture.

<sup>b</sup>Observed phenology means the model uses remote sensing data to determine leaf area index (LAI) and gross primary productivity (GPP). Semi-prognostic means that remote sensing data is used to specify either LAI or GPP, but not both.

<sup>c</sup>GPP model types: EK (enzyme kinetic) and LUE (light use efficiency).

## 4. Conclusions

[42] None of the models in this study match estimated GPP within the range of uncertainty of observed fluxes. On average, the models achieved good performance for only 12% of the simulations. Two models achieved overall marginal performance, matching estimated GPP within roughly two times the uncertainty. Our first hypothesis proved false: we found no statistically significant differences in performance due to model structure, mainly due to the large spread in performance among models and across sites. The models in our study reproduced the observed seasonal pattern with little or no GPP in winter and peak GPP in summer, but did not capture the observed GPP magnitude. We found, on average, that models overestimated GPP in spring and fall and underestimated GPP in summer. Our second hypothesis proved true: model performance depended on how models represented the GPP response to changing environmental conditions. We identified three areas of model improvement: simulated LUE, low temperature response function, and GPP response under dry conditions.

[43] The poor overall model performance resulted primarily from inadequate representation of observed LUE. Simulated LUE is controlled by the leaf-to-canopy scaling strategy and a small set of model parameters that define the maximum potential GPP, such as  $\epsilon_{\max}$  (light use efficiency),  $V_{cmax}$  (unstressed Rubisco catalytic capacity) or  $J_{\max}$  (the maximum electron transport rate). The temperature, humidity, and drought scaling factors determined temporal variability in simulated GPP, but the LUE parameters determined the magnitude of simulated GPP. To improve simulated GPP, model developers should focus first on improving the leaf-to-canopy scaling and the values of those model parameters that control the LUE.

[44] Many models overpredicted GPP under dry conditions, explaining why, on average, models performed worse at grassland and savanna sites than at forest sites. The importance of this to model performance increases at sites where drier conditions occur more frequently. Since dry conditions occur more frequently at grassland and savanna sites than at forest sites, models tended to perform worse at grassland and savanna sites compared to forest sites. Improving how models simulate soil moisture, drought stress, or humidity stress can improve simulated GPP under dry conditions.

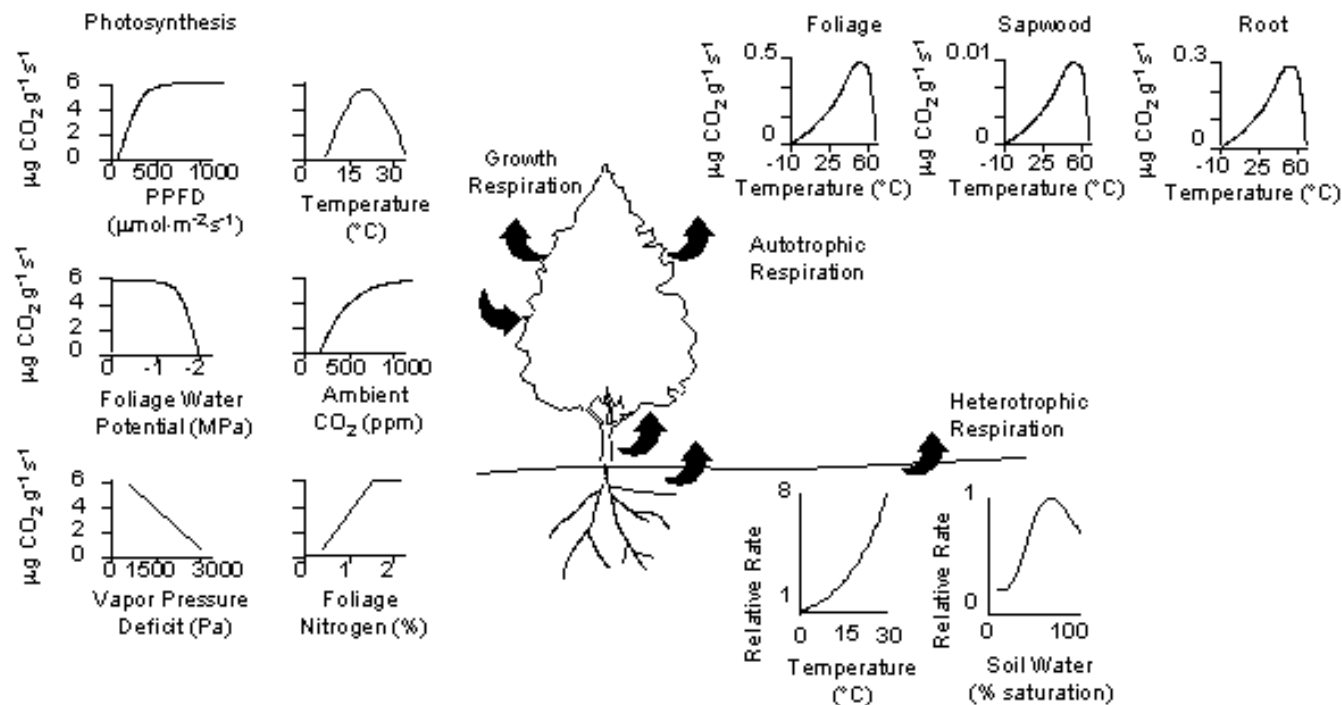
[45] Many models overpredicted GPP under cold conditions, partly explaining the positive bias in simulated GPP in winter, spring, and fall. The estimated GPP completely shut down for daily average temperatures less than  $-6^{\circ}\text{C}$ , but the  $Q_{10}$  formulation used by many models did not shut down GPP under cold or frozen conditions. The simulated GPP started too early in spring and persisted too late in fall, resulting in a positive bias and phasing errors in phenology. Using an ensemble mean can cancel out errors in phenology, but does not cancel out bias. Improving or imposing a low temperature inhibition function in the GPP model will resolve the problem.

# Good News

Now there are a variety of system models that predict the magnitudes and dynamics of ecosystem properties. Each of these models was carefully constructed with sound algorithms from meteorological, hydrological, ecological, biogeochemical, and/or statistical principles. As a result, **they are complex in terms of the number of processes factored, as well as regarding the inter-connections among the processes.** Understanding and applying these models are not easy due to their complexity. **Fortunately, almost all ecosystem models were developed with a few common algorithms.** For example, Farquhar's photosynthesis equation, the Ball–Berry stomatal conductance algorithm, Michaelis–Menten kinetics, temperature-dependent respiration in the form of Q10, and energy balance are widely used. This book is designed to describe and explain the major biophysical and empirical modules that have been used in ecosystem models. Understanding these fundamental algorithms will speed up the application of system models. For model developers, knowledge about each of the crucial modules, including their varieties, behaviors and parameterization, model performances, and their strengths and limitations, is essential to improving and advancing their work. For example, a simple Q10 algorithm based on exponential equation (Chapter 3) has been widely used in many ecosystem models for calculating respiration, yet there are many other forms that may provide more realistic predictions, albeit requiring different sets of parameters. (Chen 2020, Preface)

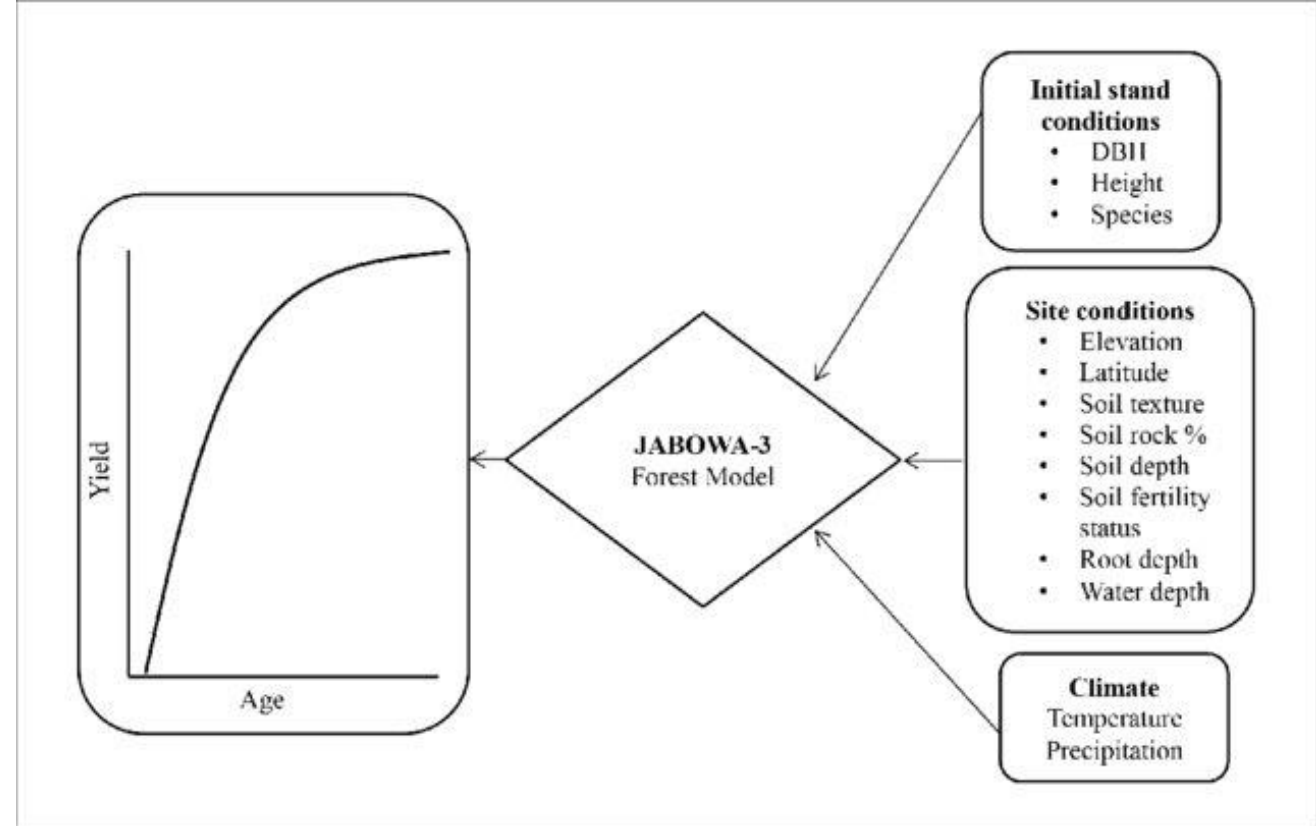
# Community Land Model (CML)

## Ecosystem Carbon Balance



# Computer Era models

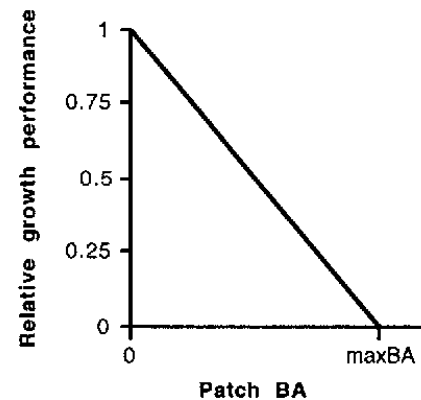
- Increasing number of variables
- Mostly empirical relationships
- Climatic, soil, disturbances, management as regulations included
- Interactions among components (e.g., species, soil-plants) are considered
- Example: JOBAWA, FORET models (a.k.a. GAP models)



Ashraf, M. I., Bourque, C. P. A., MacLean, D. A., Erdle, T., & Meng, F. R. (2012). Using JABOWA-3 for forest growth and yield predictions under diverse forest conditions of Nova Scotia, Canada. *The Forestry Chronicle*, 88(6), 708-721.

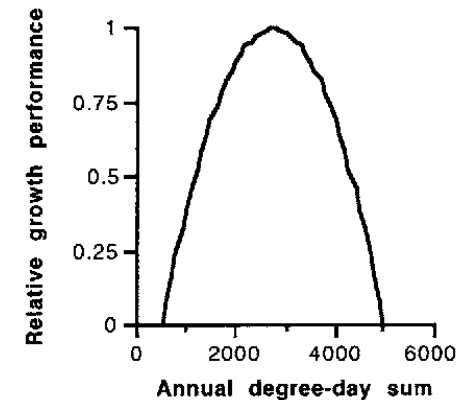
a)

**Crowding-dependent growth performance**



b)

**Temperature-dependent growth performance**



## 9.4 Photosynthesis

Photosynthesis in  $C_3$  plants is based on the model of *Farquhar et al. (1980)*. Photosynthesis in  $C_4$  plants is based on the model of *Collatz et al. (1992)*. *Bonan et al. (2011)* describe the implementation, modified here. In its simplest

form, leaf net photosynthesis after accounting for respiration ( $R_d$ ) is

$$A_n = \min(A_c, A_j, A_p) - R_d. \quad (9.2)$$

The RuBP carboxylase (Rubisco) limited rate of carboxylation  $A_c$  ( $\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) is

$$A_c = \left\{ \begin{array}{ll} \frac{V_{c \max}(c_t - \Gamma)}{c_t + K_c(1 + o_t/K_o)} & \text{for } C_3 \text{ plants} \\ V_{c \max} & \text{for } C_4 \text{ plants} \end{array} \right\} \quad c_i - \Gamma \geq 0. \quad (9.3)$$

The maximum rate of carboxylation allowed by the capacity to regenerate RuBP (i.e., the light-limited rate)  $A_j$  ( $\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) is

$$A_j = \left\{ \begin{array}{ll} \frac{J_x(c_t - \Gamma)}{4c_t + 8\Gamma} & \text{for } C_3 \text{ plants} \\ \alpha(4.6\phi) & \text{for } C_4 \text{ plants} \end{array} \right\} \quad c_i - \Gamma \geq 0. \quad (9.4)$$

The product-limited rate of carboxylation for  $C_3$  plants and the PEP carboxylase-limited rate of carboxylation for  $C_4$  plants  $A_p$  ( $\mu \text{ mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) is

$$A_p = \left\{ \begin{array}{ll} 3T_p & \text{for } C_3 \text{ plants} \\ k_p \frac{c_t}{P_{atm}} & \text{for } C_4 \text{ plants} \end{array} \right\}. \quad (9.5)$$



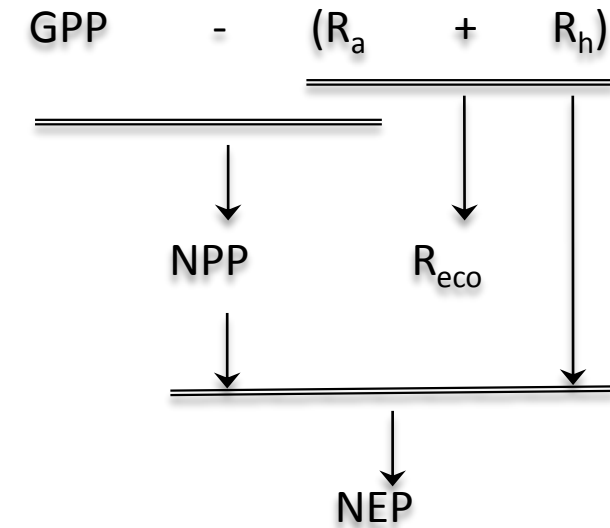
For example

1) Michaelis-Menten kinetics for photosynthesis (GPP)

$$P_n = \frac{\alpha \cdot PAR \cdot P_m}{\alpha \cdot PAR + P_m} - R_d \quad [2.2]$$

But with different varieties

$$P_n = \frac{1}{2 \cdot \beta} \left( \alpha \cdot PAR + P_m - \sqrt{(\alpha \cdot PAR + P_m)^2 - 4 \cdot \alpha \cdot PAR \cdot P_m \cdot \beta} \right) \quad [2.4]$$

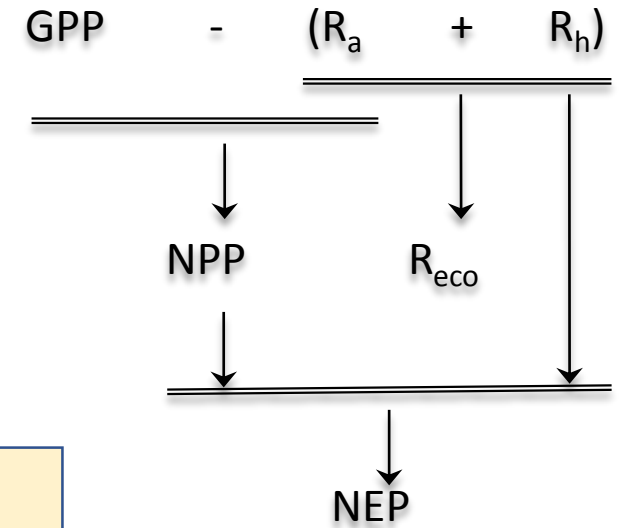


2) Q10 model for carbon loss ( $R_a$ ,  $R_h$ ,  $R_{eco}$ ) in many models

The  $Q_{10}$  model (Van't Hoff 1898):

$$Q_{10} = \left( \frac{R_2}{R_1} \right)^{\left( \frac{10}{T_2 - T_1} \right)}$$

Brief history  
Principles  
Strengths/weakness  
Model demonstrations  
...



But also with different varieties

$$R = R_0 \cdot e^{\beta_0 \cdot T} \cdot e^{\beta_1 \cdot \theta} \cdot \beta_2 \cdot T \cdot \theta$$

[3.17]

## PnET-II model

Vol. 5: 207–222, 1995

CLIMATE RESEARCH  
Clim Res

Published December 7

### Predicting the effects of climate change on water yield and forest production in the northeastern United States

John D. Aber<sup>1,\*</sup>, Scott V. Ollinger<sup>1</sup>, C. Anthony Federer<sup>2</sup>, Peter B. Reich<sup>3</sup>, Michael L. Goulden<sup>4</sup>, David W. Kicklighter<sup>5</sup>, Jerry M. Melillo<sup>5</sup>, Richard G. Lathrop, Jr<sup>6</sup>

**Soil respiration:** This routine was not present in the original model and is included here to allow a system-level carbon balance calculation. It does *not* contain a complete soil carbon budget which would be driven by litter deposition and associated decomposition terms. Rather, it uses a generalized soil respiration equation developed for temperate zone forests by Kicklighter et al. (1994). Soil respiration is assumed to include both microbial respiration associated with decomposition and respiration by live roots. That equation, derived using measured, plot-level soil CO<sub>2</sub> flux data from a wide variety of sites, is :

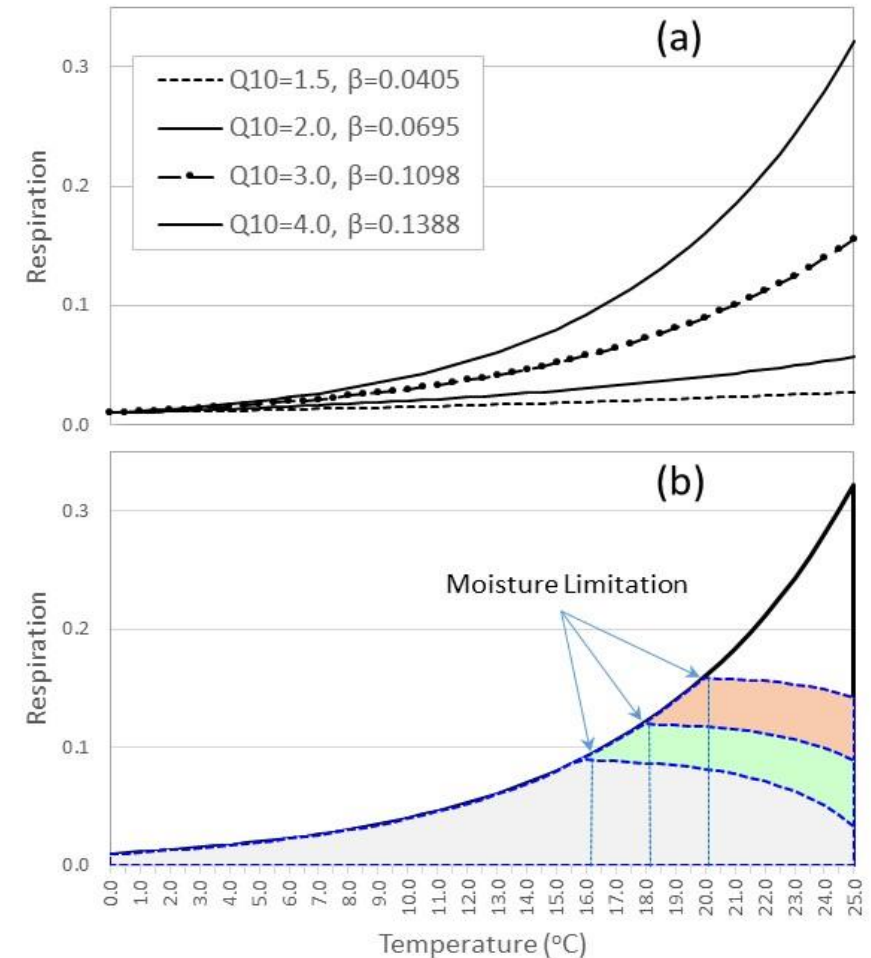
$$\text{Soil respiration (g C m}^{-2} \text{ mo}^{-1}) = 27.46 e^{0.06844t} \quad (4)$$

where  $t$  is the mean monthly temperature (°C). Data from the Harvard Forest site represent approximately 24% of the total used to derive this equation. The remaining data come from a widely distributed set of temperate zone forests (see Kicklighter et al. 1994 for full description).

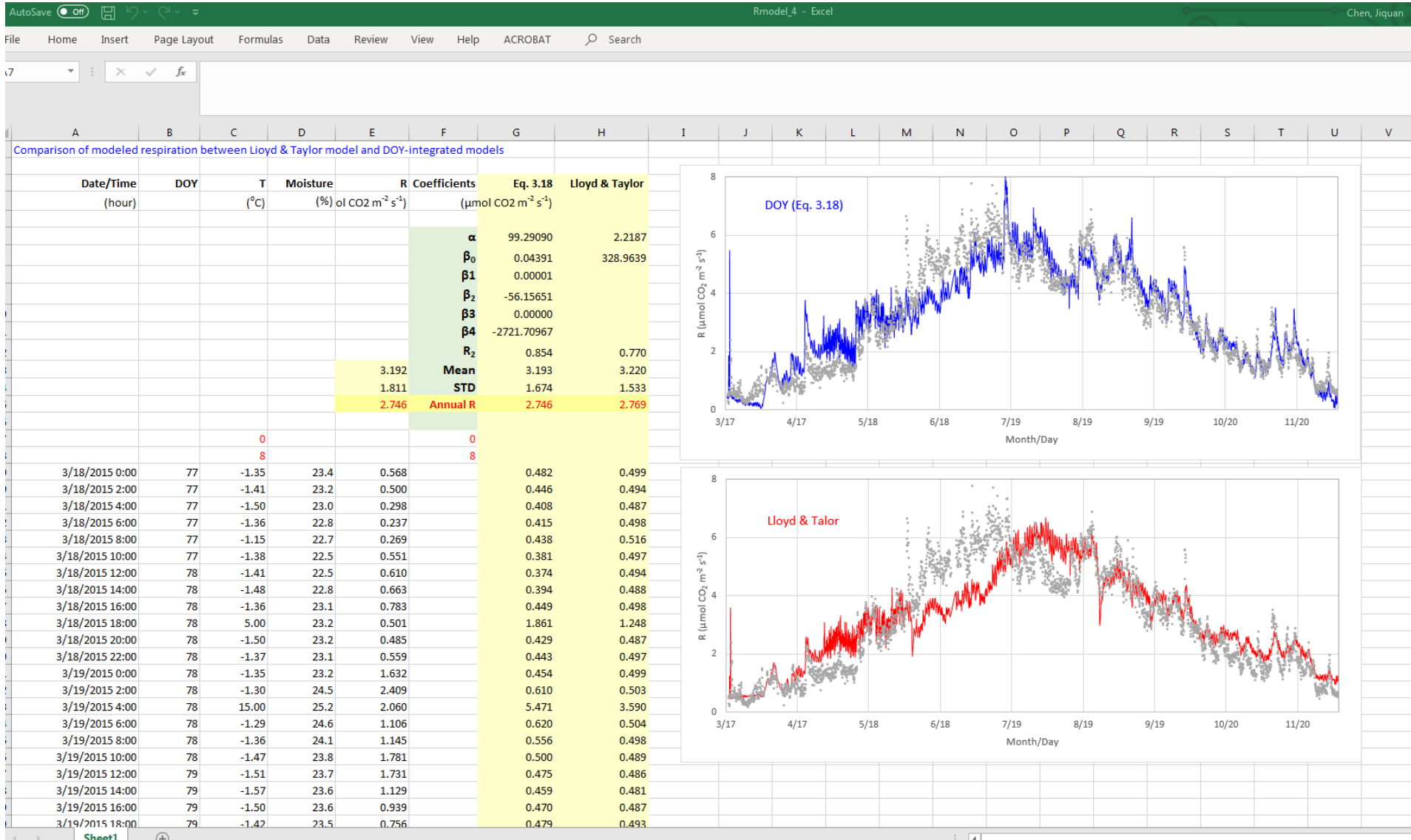
It is also critical to learn how respiration is measured!



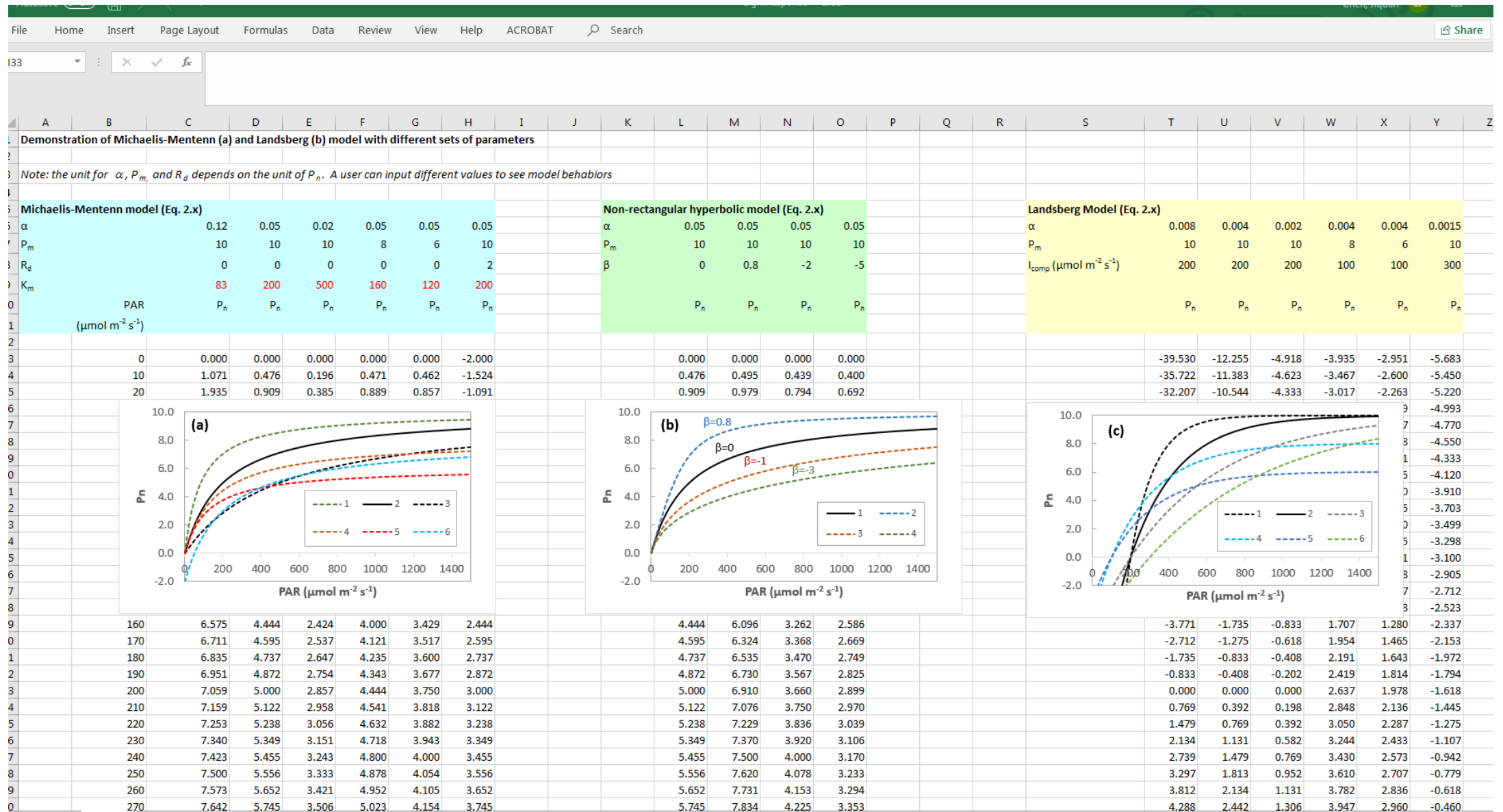
**Figure 3-1.** Schematic illustration of change in respiration with temperature by an exponential function (Eq. 3.3) for four  $Q_{10}$  values (a). The exponential increase of respiration can be limited by other ecological resources such as moisture (b). The respiration reduction due to low moisture can be linear, polynomial, Gamma, logistic, or take other forms. The threshold point can be empirically determined for a site or a specific time period.



# Hands on exercise is an effective way to learn!



# Spreadsheet modeling: A demonstration of light response curve



# In Sum

The past five decades have witnessed a rapid growth of computer models for simulating ecosystem functions and dynamics. This has been fueled by the availability of remote sensing data, computation capability, and cross-disciplinary knowledge. These models contain many submodules for simulating different processes and forcing mechanisms, albeit it has become challenging to truly understand the details due to their complexity. Most ecosystem models, fortunately, are rooted in a few core biophysical foundations, such as the widely recognized Farquhar model, Ball-Berry-Leuning and Medlyn family models, Penman-Monteith equation, Priestley-Taylor model, and Michaelis-Menten kinetics. After an introduction of biophysical essentials, four chapters present the core algorithms and their behaviors in modeling ecosystem production, respiration, evapotranspiration, and global warming potentials. Each chapter is composed of a brief introduction of the literature, in which model algorithms, their assumptions, and performances are described in detail. Spreadsheet (or Python codes) templates are included in each chapter for modeling exercises with different input parameters as online materials, which include datasets, parameter estimation, and real-world applications (e.g., calculations of global warming potentials). Users can also apply their own datasets. The materials included in this volume serve as effective tools for users to understand model behaviors and uses with specified conditions and in situ applications.

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# Structural Features

- Five thematic areas: biophysical foundations, photosynthesis (gross primary production or GPP), respiration (autotrophic, heterotrophic, soil, ecosystem), evapotranspiration (ET), and global warming potentials (GWP)
- Update reading materials (i.e., not just limited to the textbook!)
- Hands-on exercises during the classes
- Online resources (data, models, short videos, etc.)
- Critical references
- Different versions of the models (upon request!)

# Why?

A number of questions usually arise when a student starts to consider quantitative models for fitting their experimental data, achieving a specific study objective, or testing a hypothesis. Common questions include: Which model should I use, and why? Are there alternative options? What are the meanings of the parameters in each model? What values should I use as parameters? And how do I construct the model for my study? My answer to each of these legitimate questions often is, “It depends.” This is because every model, biophysically or empirically, was developed for specific conditions or under certain assumptions. In ecosystem studies, no single model could be used to answer the full range of scientific questions. They are based on crucial ecological and physical processes and should not be assumed to work “perfectly” in all ecosystem types, under all kinds of circumstances, and across all spatial and temporal scales. Yet, the answer “It depends” often adds to the confusion, until algorithms are well explained, with history, rationales, and applications. I also find that demonstrative examples with real-world data are very helpful. Over 30 model templates in Excel Spreadsheets or Python codes are provided here for demonstrations and uses. Above needs for context and background were the primary motivation behind writing this book.

A second motivation stemmed from the unprecedented growth in the number and complexity of ecosystem models developed over the past 40 years. Now there are a variety of system models that predict the magnitudes and dynamics of ecosystem properties. Each of these models was carefully constructed with sound algorithms from meteorological, hydrological, ecological, biogeochemical, and/or statistical principles. As a result, they are complex in terms of the number of processes factored, as well as regarding the inter-connections among the processes. Understanding and applying these models are not easy due to their complexity. Fortunately, almost all ecosystem models were developed with a few common algorithms. For example, Farquhar’s photosynthesis equation, the Ball-Berry stomatal conductance algorithm, Michaelis-Menten kinetics, temperature-dependent respiration in

# Unit and its different expressions are critical

Additional information is available upon request

## The challenges: Carbon as an

- **Terms:** NPP, NEP, GPP,  $P_s$ ,  $R_e$ , NEE,  $NEE_C$ , storage,  $C_{soil}$ , yield, production, etc.
- **Unit:**  $g \cdot m^{-2}$ ;  $MG \cdot ha^{-1} \cdot yr^{-1}$ ; Ton/ha,  $umol \cdot m^{-2} \cdot yr^{-1}$
- **Conversion:** C vs  $CO_2$ ; C vs  $CH_4$ ; C vs bio
- **Reasonable range of global ecosystems**

## Tables for Weights and Measurement: Crops

William J. Murphy  
Department of Agronomy

These tables give weights per bushel, weights of grain by volume, moisture conversion and planting rates.

Table 1  
Weights per bushel

- Alfalfa  
60 pounds per bushel
- Barley  
48 pounds per bushel
- Clover, Alsike  
60 pounds per bushel
- Clover, Crimson  
60 pounds per bushel
- Clover, Ladino  
60 pounds per bushel

# Table 1. Basic units

Name	Notation/Symbol	Unit
Length		m
Mass	M	kg
Acceleration	a	$\text{m s}^{-2}$
Force	N	$\text{kg m s}^{-2}$
Energy	E	J
Power	P	W
Work	W	$\text{kg m}^2 \text{s}^{-2}$
Frequency	f	Hz
Pressure	P	Pa
Electric charge	Q	C
Electric potential difference	U	V
Capacitance	C	F
Electric resistance	R	$\Omega$
Electric conductance	G	S
Magnetic flux	$\Phi$	Wb
Magnetic flux density	B	T

## Most common and useful unit conversions

In this paragraph we go over some of the most common and useful unit conversions broadly used in science.

### 1. Temperature

Temperature can be expressed in Celsius (SI), Fahrenheit, or Kelvin (°C, F, and K, respectively). The conversions are the following:

$$^{\circ}\text{C} \rightarrow F = ^{\circ}\text{C} \cdot \frac{9}{5} + 32 \quad (1.1)$$

$$F \rightarrow ^{\circ}\text{C} = F - 32 \cdot \frac{5}{9} \quad (1.2)$$

$$^{\circ}\text{C} \rightarrow K = ^{\circ}\text{C} + 273.15 \quad (1.3)$$

$$K \rightarrow ^{\circ}\text{C} = K - 273.15 \quad (1.4)$$

$$K \rightarrow F = (K - 273.15) \cdot \frac{9}{5} + 32 \quad (1.5)$$

$$F \rightarrow K = (F - 32) \cdot \frac{5}{9} + 273.15 \quad (1.6)$$

### 2. Area

Area is usually expressed in both m<sup>2</sup> and hectare (ha). The conversions between the two are the following:

$$m^2 \rightarrow ha = m^2 \div 10,000 \quad (2.1)$$

$$ha \rightarrow m^2 = ha \cdot 10,000 \quad (2.2)$$

### 3. Mass

Generally, in the SI mass is expressed in grams (g) or their multiples and submultiples (e.g., kg, mg, respectively):

$$g \rightarrow kg = g \div 1,000 \quad (3.1)$$

$$g \rightarrow Mg = g \div 1,000,000 \quad (3.2)$$

However, some fields require it to be expressed in moles (mol). The conversion between the two is given

by the following equations:

$$\frac{m_s(g)}{N_s(mol)} = M_s(g/mol) \quad (3.3)$$

where  $m_s$  is the mass (g) of the substance,  $N_s$  is the quantity (mol) of the substance, and  $M_s$  is the molar mass (g/mol) of the substance, which is given by the sum of the standard atomic weight of the atoms composing it.  $M_s$  must be multiplied by the molar mass constant (i.e., 1 g/mol).

Moreover, in some fields (e.g., agriculture, forestry, ecology, etc.) it is very useful to report information of the mass per unit area. Depending on the spatial scale a study is referred to, the units can vary from as small as  $\mu\text{mol}/\text{cm}^2$  up to as big as Mg/ha. Here below, we show one of the most common unit conversion in environmental studies that can be applied to both local and global scale:

$$a (g \cdot m^{-2}) \rightarrow b (kg \cdot m^{-2}) = a \div 1,000 \quad (3.4)$$

$$a (g \cdot m^{-2}) \rightarrow b (kg \cdot ha^{-1}) = a \times 10 \quad (3.5)$$

$$a (kg \cdot m^{-2}) \rightarrow b (kg \cdot ha^{-1}) = a \div 10,000 \quad (3.6)$$

$$a (kg \cdot m^{-2}) \rightarrow b (Mg \cdot ha^{-1}) = a \times 10 \quad (3.7)$$

$$a (g \cdot m^{-2}) \rightarrow b (Mg \cdot ha^{-1}) = a \div 100 \quad (3.8)$$

### 1. Time

Time can be expressed in different ways — e.g., seconds (s), minutes (min), hours (h), days (d), months, years (yr) — depending on the needs. Here are some examples and conversions:

$$a (s) \rightarrow b (min) = a \div 60 \quad (4.1)$$

$$a (s) \rightarrow b (h) = a \div 3,600 \quad (4.2)$$

$$a (h) \rightarrow b (d) = a \div 24 \quad (4.3)$$

$$a (d) \rightarrow b (month) = a \div \sim 30 \text{ (or } 30.417) \quad (4.4)$$

$$a (d) \rightarrow b (yr) = a \div 365 \quad (4.5)$$

## Energy

Lastly, we introduce some basic relationships between energy (E), force (N), power (P), and calorie (cal):

$$1E(J) \rightarrow 1N(kg \cdot m \cdot s^{-2}) = 1N \times 1m = 1kg \cdot m^2 \cdot s^{-2} \quad (5.1)$$

$$1E(J) \rightarrow 1P(W) = 1P \times 1s = 1W \cdot s \quad (5.2)$$

$$1W \cdot s \rightarrow 1kW \cdot h = 1W \div 1,000 \cdot s \div 3,600 = 3.6 \times 10^6 \text{Joule} \quad (5.3)$$

$$1cal(J) = \text{heat required to } \uparrow 1g_{H_2O} \text{ by } 1^\circ C = 4.186J \quad (5.4)$$

## Energy variables

In this paragraph we introduce some of the variables used in energy studies and divided into five major groups, such as, radiation and light, photometry, heat, energy, and electromagnetism.

**Table 2** Radiation and light energy related variables

Name	Notation/Symbol	Unit
Longwave-, shortwave-, net-radiation	$R_L, R_S, R_n$	$W m^{-2}$
Albedo	$\alpha$	unitless or %
Radiative forcing	RF	$W m^{-2}$
Normalized radiative forcing by mass	NRFM	$W g^{-1}$
Equilibrium climate sensitivity relative to albedo	$\lambda_{alb}$	$K (W m^{-2})^{-1}$
Solid angle	$\Omega$	Sr or $m^2 m^{-2}$
Wavelength	$\lambda$	nm
Photosynthetic photon flux density	PPFD	$mol (m^2 s)^{-1}$
Absorbed photosynthetically active radiation	APAR	$mJ (m^2 day)^{-1}$
Fraction of APAR	FAPAR	Fractional (unitless)
Quantum yield of fluorescence	$\Phi_F$	Fractional (unitless)
Solar induced fluorescence	SIF	$mW (m^2 sr nm)^{-1}$
Radiant energy density	$w_e$	$J m^{-3}$
Radiant flux	$\Phi_e$	$J s^{-1}$
Spectral flux	$\Phi_e, \nu$	$W Hz^{-1}$
Radiance	$L_e, \Omega$	$W sr^{-1} m^{-2}$
Flux density	$E_e$	$W m^{-2}$
Radiosity	$J_e$	$W m^{-2}$
Radiant exitance	$M_e$	$W m^{-2}$
Radiant exposure	$H_e$	$J m^{-2}$

$\lambda_{alb}$  is calculated as  $\Delta T_s / (\Delta F - \Delta R)$ , where  $\Delta T_s$  is the surface temp change,  $\Delta F$  is the RF due to albedo change, and  $\Delta R$  is the net radiative flux at TOA (Davin *et al* 2007).

NRFM is the direct RF for a specific gas in the atmosphere (Akbari *et al* 2009, Forster *et al* 2007)

**Table 3** Photometry energy related variables

Name	Notation/Symbol	Unit
Luminous energy	$Q_v$	lm s
Luminous flux	$\Phi_v$	lm
Luminous intensity	$I_v$	cd
Luminance	$L_v$	$cd m^{-2}$
Illuminance	$E_v$	lx
Luminous exitance	$M_v$	$lm m^{-2}$
Luminous exposure	$H_v$	lx s
Luminous energy density	$\omega_v$	$lm s m^{-3}$
Luminous efficacy	$K$	$lm W^{-1}$

## Table 4 Heat energy related variables

Name	Notation/Symbol	Unit
Ground heat storage from conduction	$R_G$	$W m^{-2}$
Sensible heat	H	$W m^{-2}$
Latent heat of vaporization	L	$mJ kg^{-1}$
Soil and air volumetric heat capacity	$C_s$ and $C_p$	$J m^{-3} \text{ } ^\circ C^{-1}$
Soil thermal conductivity	$k_s$	$W m^{-2} \text{ } ^\circ C^{-1}$
Heat capacity	C	$J K^{-1}$
Specific heat capacity	c	$J (mol K)^{-1}$
Entropy	S	$J (mol K)^{-1}$



# Table 5 Energy related variables

Name	Notation/Symbol	Unit
Energy consumption	–	kWh
Energy usage intensity	EUI	kWh m <sup>-2</sup> yr <sup>-1</sup>
Energy yield	–	MJ ha <sup>-1</sup> yr <sup>-1</sup>
Molar chemical potential	$\mu$	J mol <sup>-1</sup>
Internal Energy	U	J
Potential Energy	PE	J
Kinetic Energy	KE	J
Thermal Energy	Q	J
Free Energy	G	J
Enthalpy	H	J
Calorie	cal	J

**Table 6** Electromagnetism energy related variables

Name	Notation/Symbol	Unit
Electric charge	Q	C
Electric current	I	A
Electric current density	J	A m <sup>-2</sup>
Resistivity	$\rho$	$\Omega$ m
Electric flux	$\Phi E$	V m
Electric field strength	E	V m <sup>-1</sup>
Electric displacement field	D	C m <sup>-2</sup>
Permittivity	$\epsilon$	F m <sup>-1</sup>
Conductance	G	S
Conductivity	$\kappa$	S m <sup>-1</sup>
Magnetic field strength	H	A m <sup>-1</sup>
Inductance	L	H
Permeability	$\mu$	H m <sup>-1</sup>

# Constants

## Table 7 Constants values

E is the radiant heat energy emitted from a unit area in 1sec, and T is the temperature in K

<sup>2</sup> E is the photon energy (J s<sup>-1</sup>) and f is the wave frequency

<sup>3</sup> P and V are pressure and volume, respectively, N and T are the number of molecules and the temperature, respectively

<sup>4</sup> P and V are pressure and volume, respectively, n and T are the number of moles and the temperature

Name	Notation/Symbol	Value	Unit	Formula
Stefan-Boltzmann	$\sigma$	$5.67 \cdot 10^{-8}$	$\text{W m}^{-2} \text{K}^{-4}$	<sup>1</sup> $\sigma = E T^{-4}$
Calorie <sub>H<sub>2</sub>O</sub>	cal	4.186	J	
Speed of light in vacuum	c	$2.9979 \cdot 10^8$	$\text{m s}^{-2}$	
Planck's constant	h	$6.6261 \cdot 10^{-34}$	J s	<sup>2</sup> $h = E f^{-1}$
Boltzmann constant	k	$1.38065 \cdot 10^{-23}$	$\text{J K}^{-1}$	<sup>3</sup> $k = PV (NT)^{-1}$
Gas constant for dry air	R	8.314	$\text{J K}^{-1} \text{mol}^{-1}$	<sup>4</sup> $R = PV (nT)$

## The structure of each chapter

- 1. Concepts, history, principles, literature**
- 2. Core models and comparisons**
- 3. Datasets and model performances**
- 4. Online Supplementary Materials (models, data, codes)**
  - ✓ A unique code is given to a user)
  - ✓ In-class exercise (independent or group)
  - ✓ Online recourses (video, demos, etc.)
  - ✓ Model demonstrations
  - ✓ Homework

# Chapter 2: MODELING ECOSYSTEM PRODUCTION – An example

## 2.1 Introduction

## 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

## 2.3 The datasets for Modeling Photosynthesis

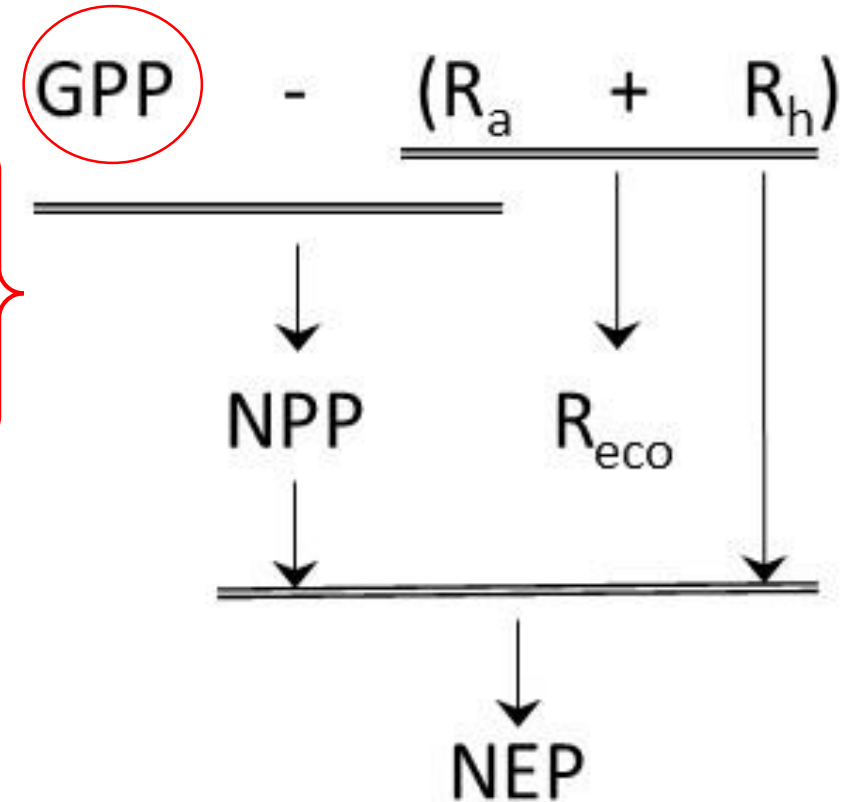
2.4.1 Light response models

2.4.2 Results from Farquhar's model

2.4.3 Results from Ball-Berry Model

2.4.4 Other models

## 2.5 Summary

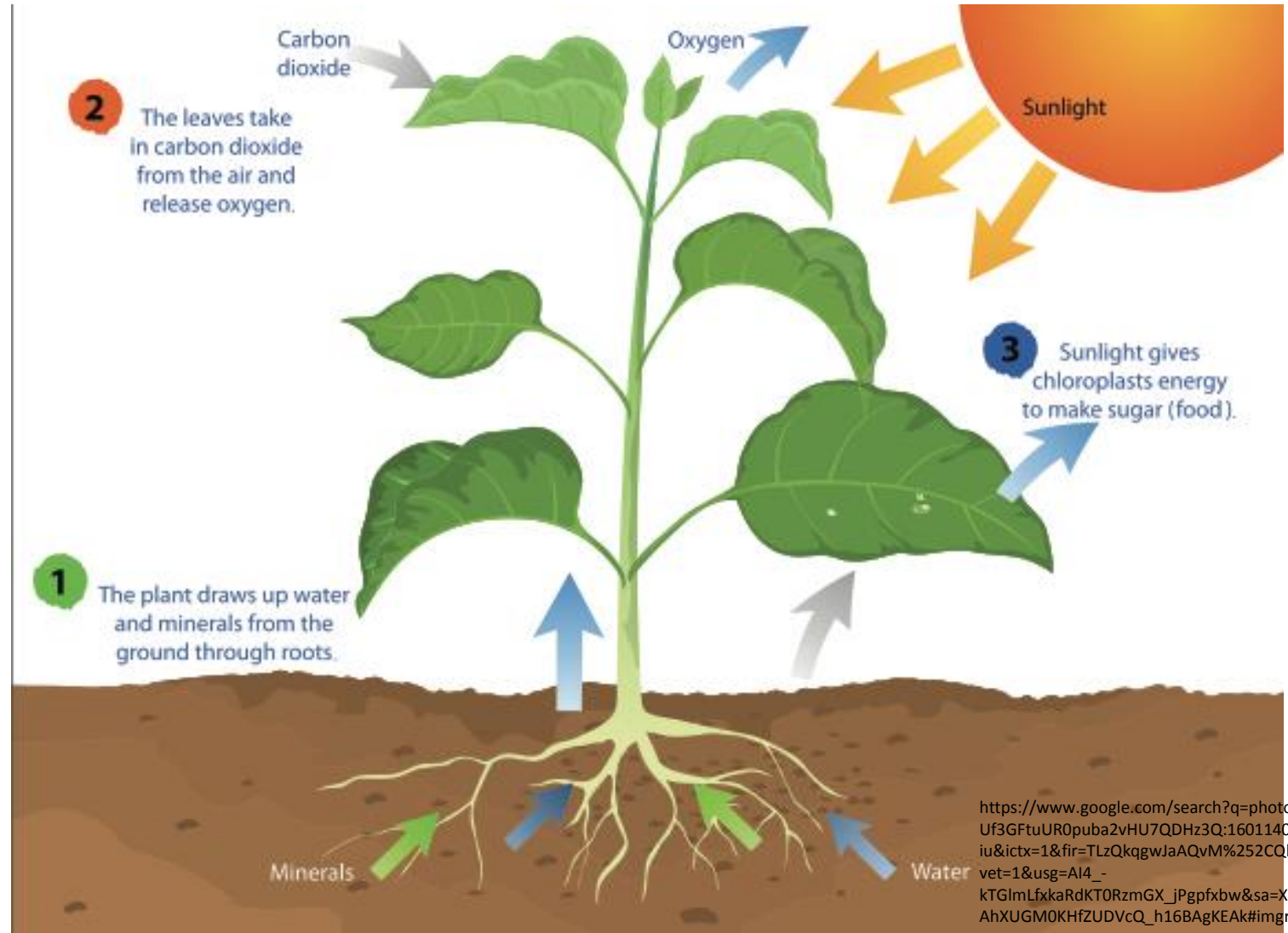


**Photosynthesis** is the first step for assimilating atmospheric CO<sub>2</sub> into organic substances in an ecosystem

- Photosynthesis is a physiological process in which plants, algae and certain bacteria convert solar energy and CO<sub>2</sub> 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=FfLLHQDgpjl>



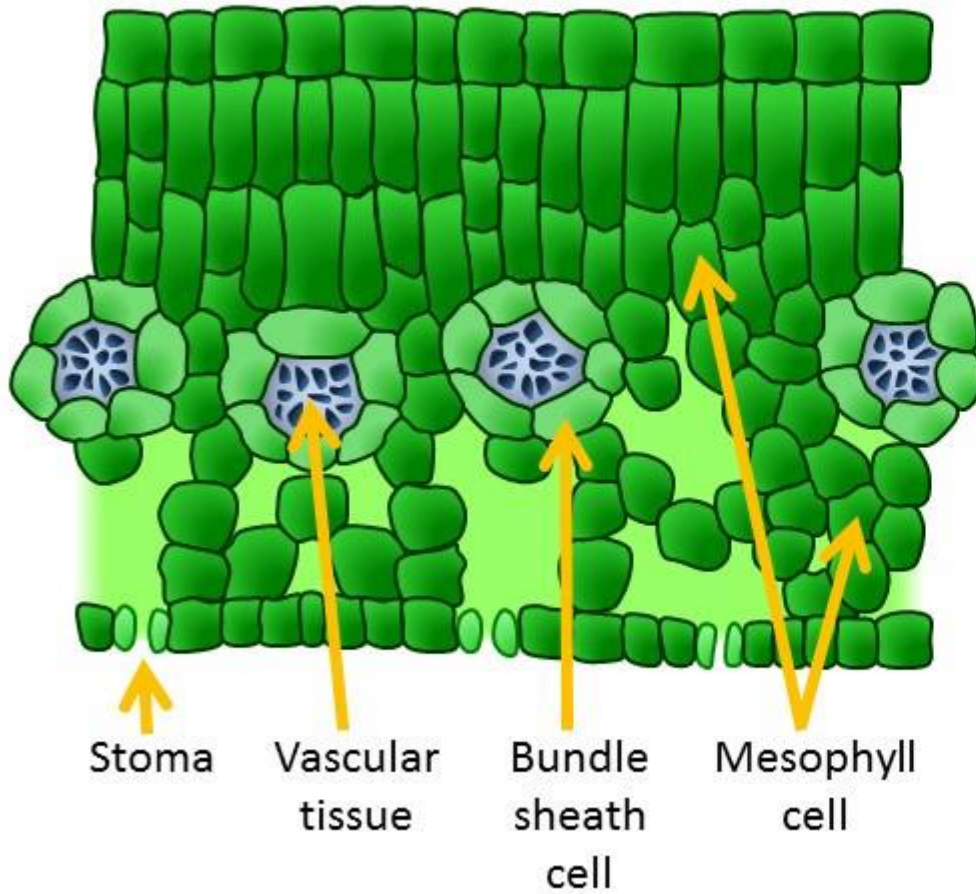
Chemical expression has several forms, including the following one:



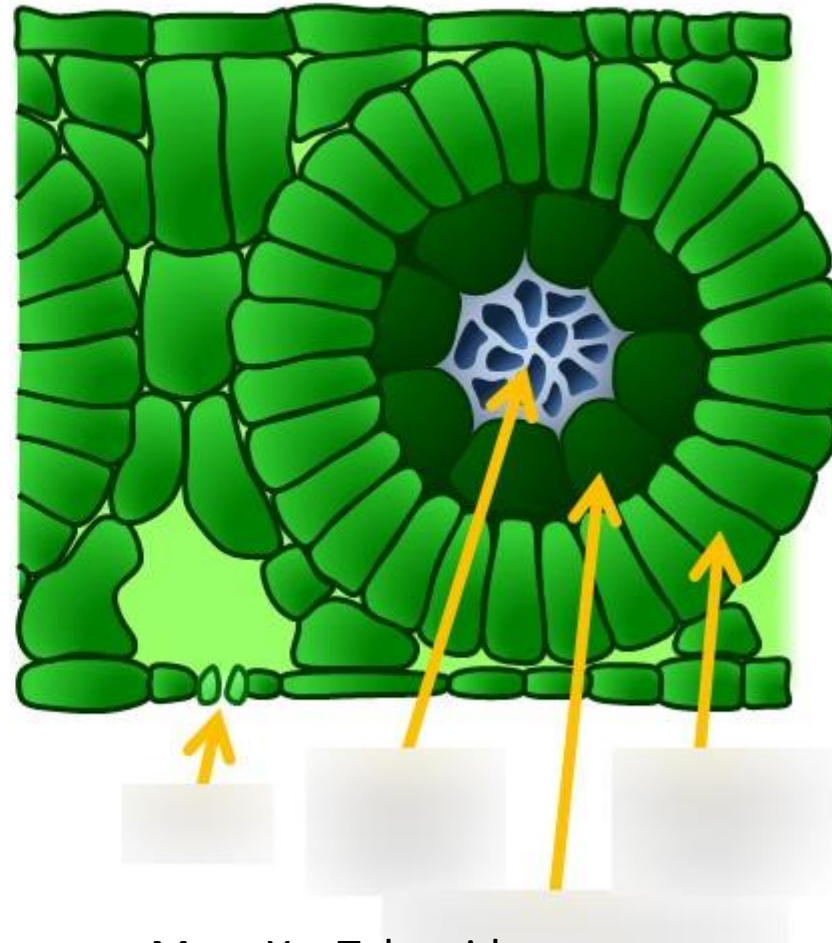
# Comparing C<sub>3</sub>, C<sub>4</sub> and CAM

<https://www.youtube.com/watch?v=13h5oC4jlsk>

## C<sub>3</sub> plant



## C<sub>4</sub> plant



## CAM

More YouTube videos:  
<https://www.youtube.com/watch?v=HbLg4IMpUa8>  
<https://www.youtube.com/watch?v=Dq38MpYOb8w>



Chemical expression has several forms, including the following one:



A-C<sub>i</sub> curve

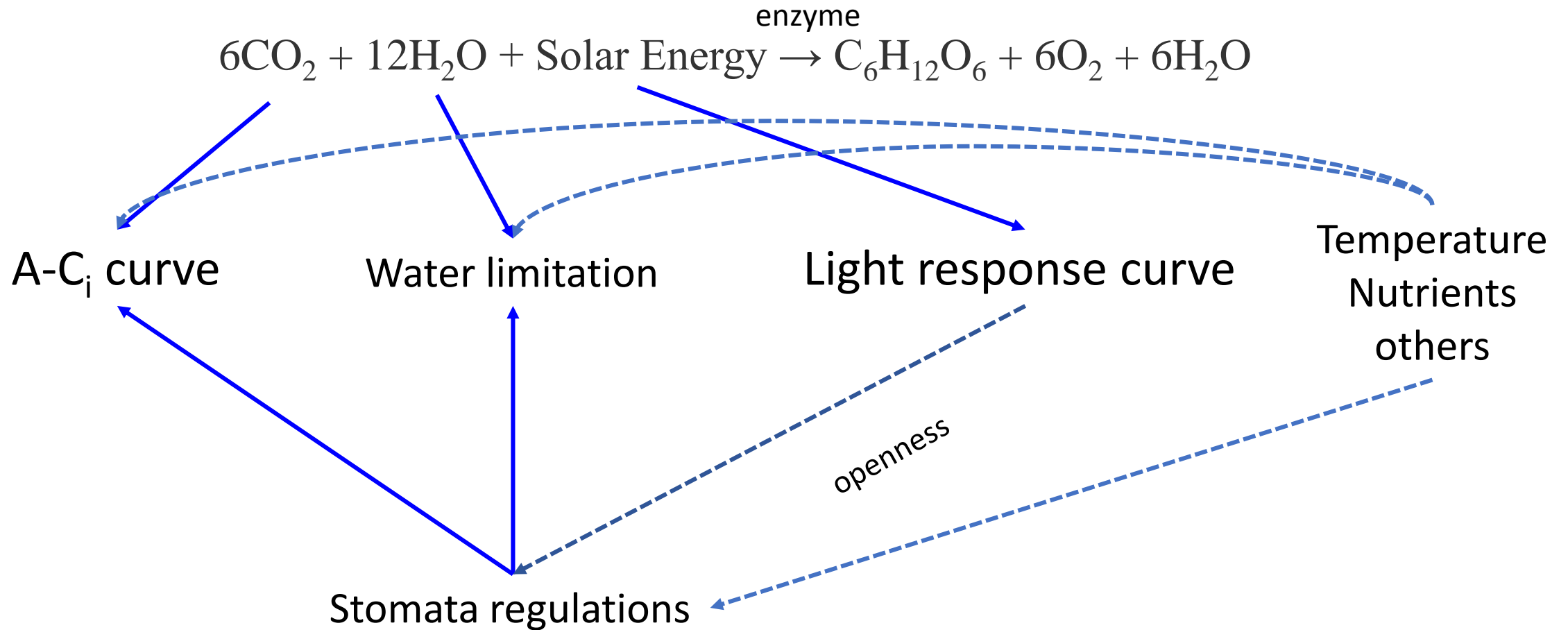
Water limitation

Light response curve

Temperature  
Nutrients  
others

Stomata regulations

openness



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



LiCor6400 (LI6800)

CO<sub>2</sub> & H<sub>2</sub>O concentration  
PAR, temperature



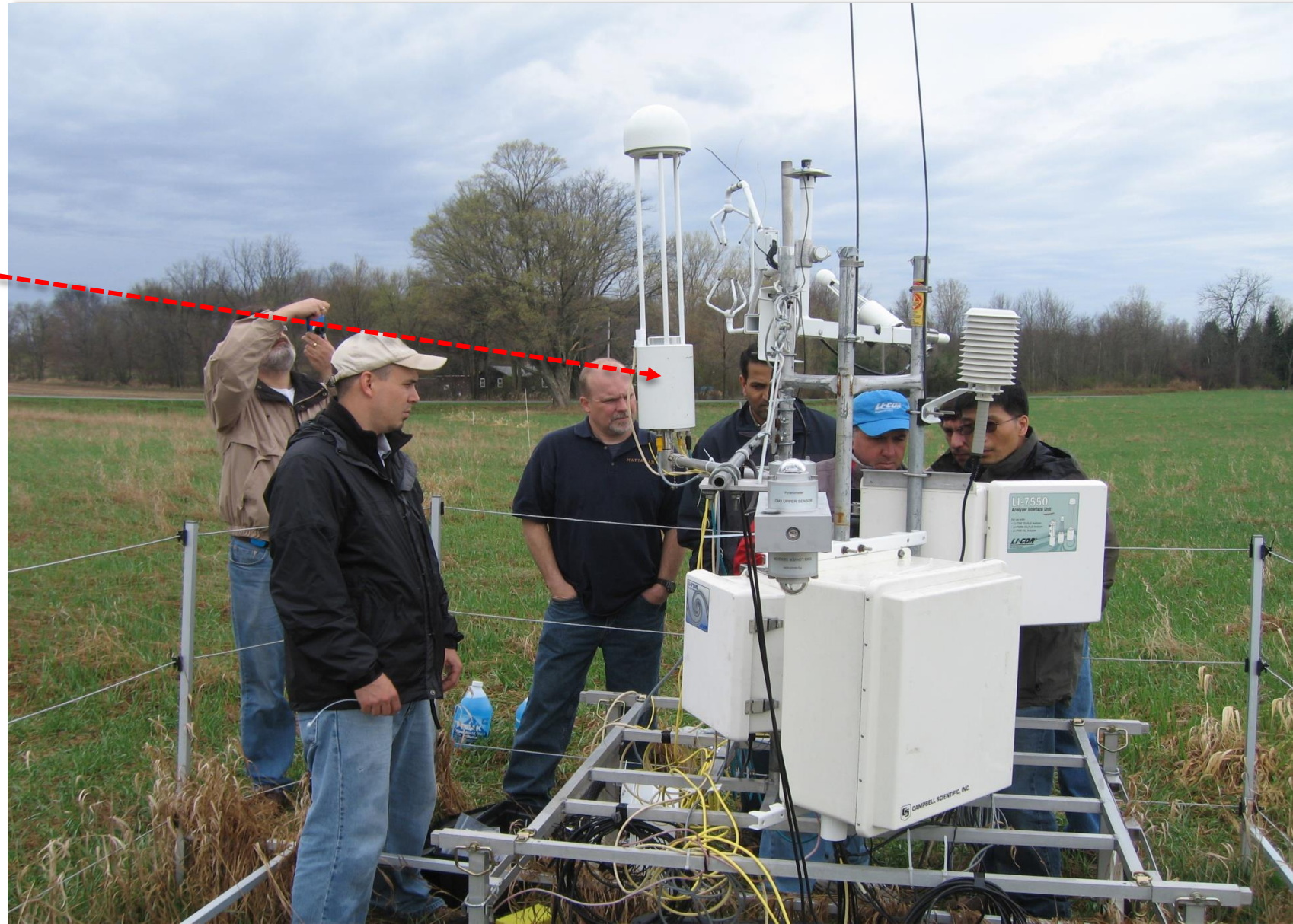
## Measuring photosynthesis: chamber-based at leaf level (continuous)



# Measuring photosynthesis: EC tower

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

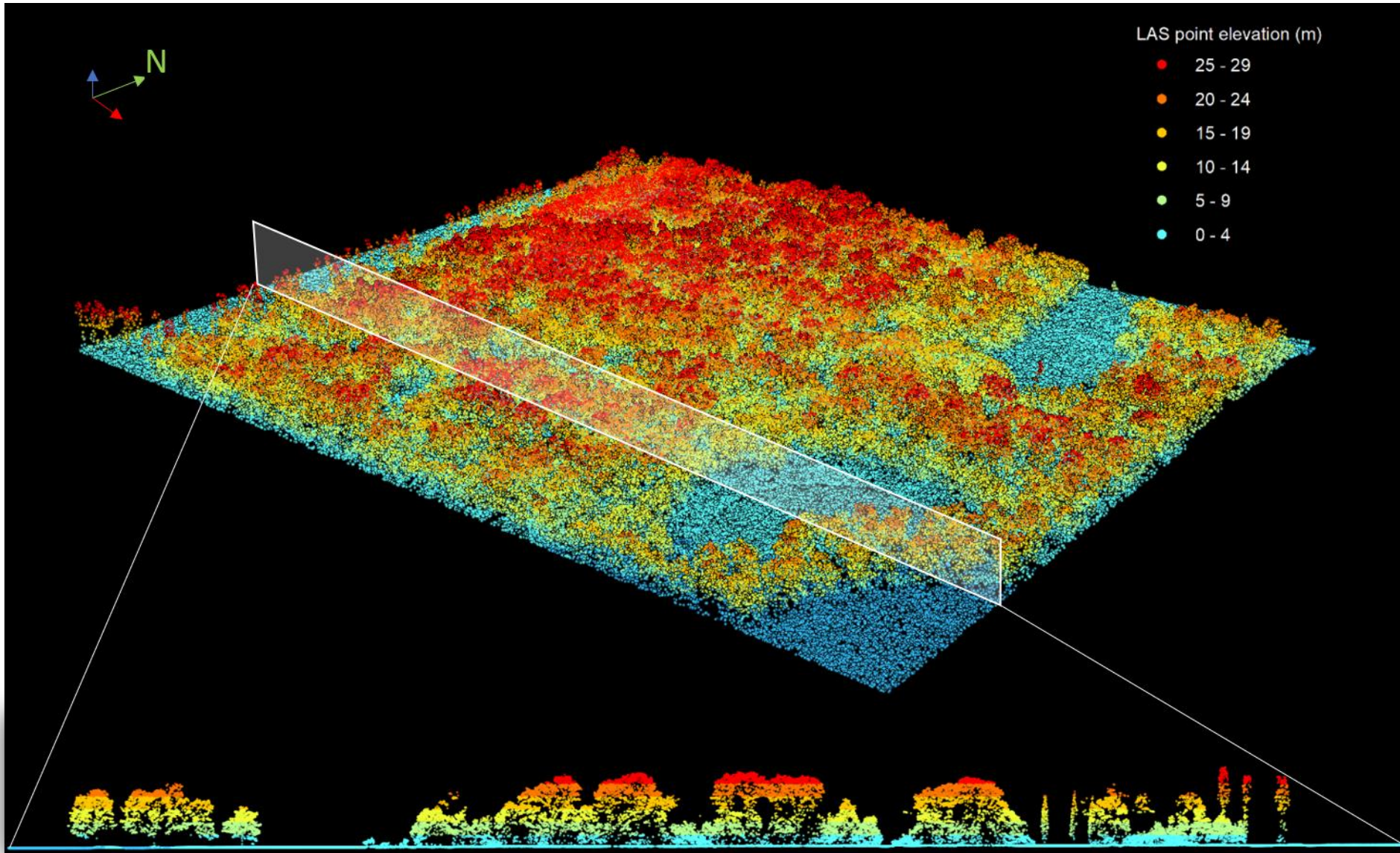
LI7700  
 $CH_4$



## Measuring photosynthesis: Biometric approach (tree ring, DBH)



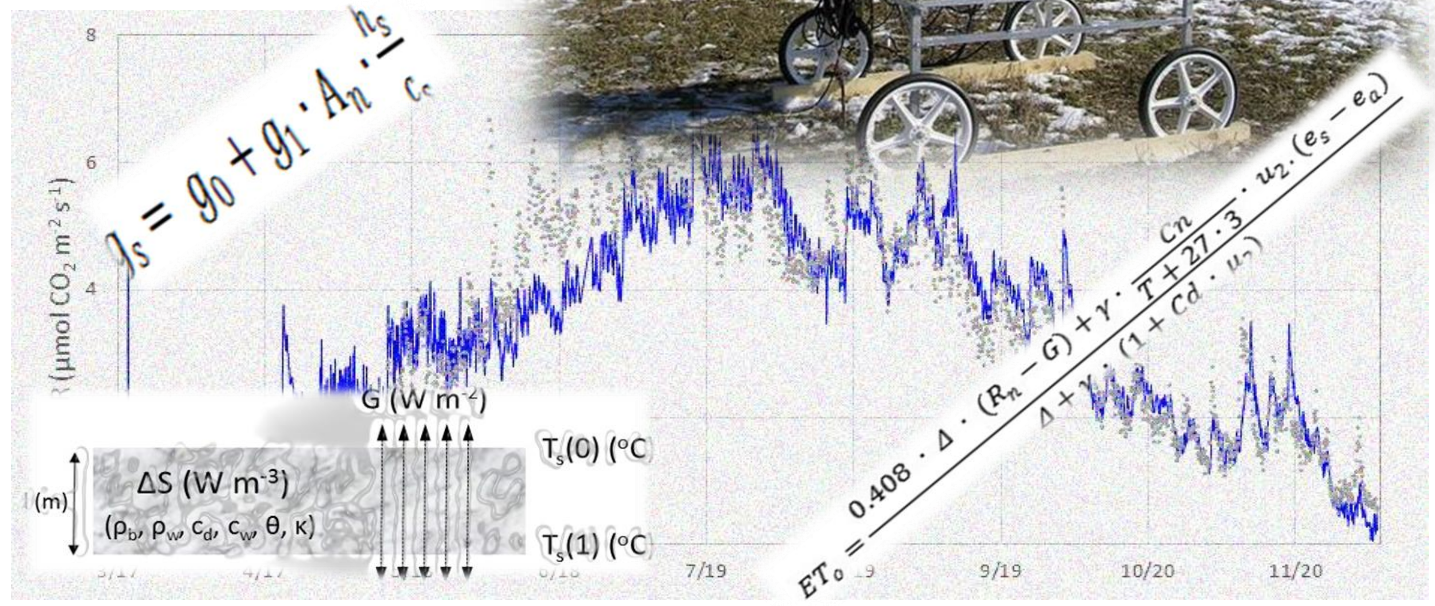
# Measuring photosynthesis: remote sensing modeling



# Measuring photosynthesis: ecosystem modeling

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

$$R = R_{10} \cdot e^{E_0 \left[ \frac{1}{56.02} - \frac{1}{T - 227.13} \right]}$$



## 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

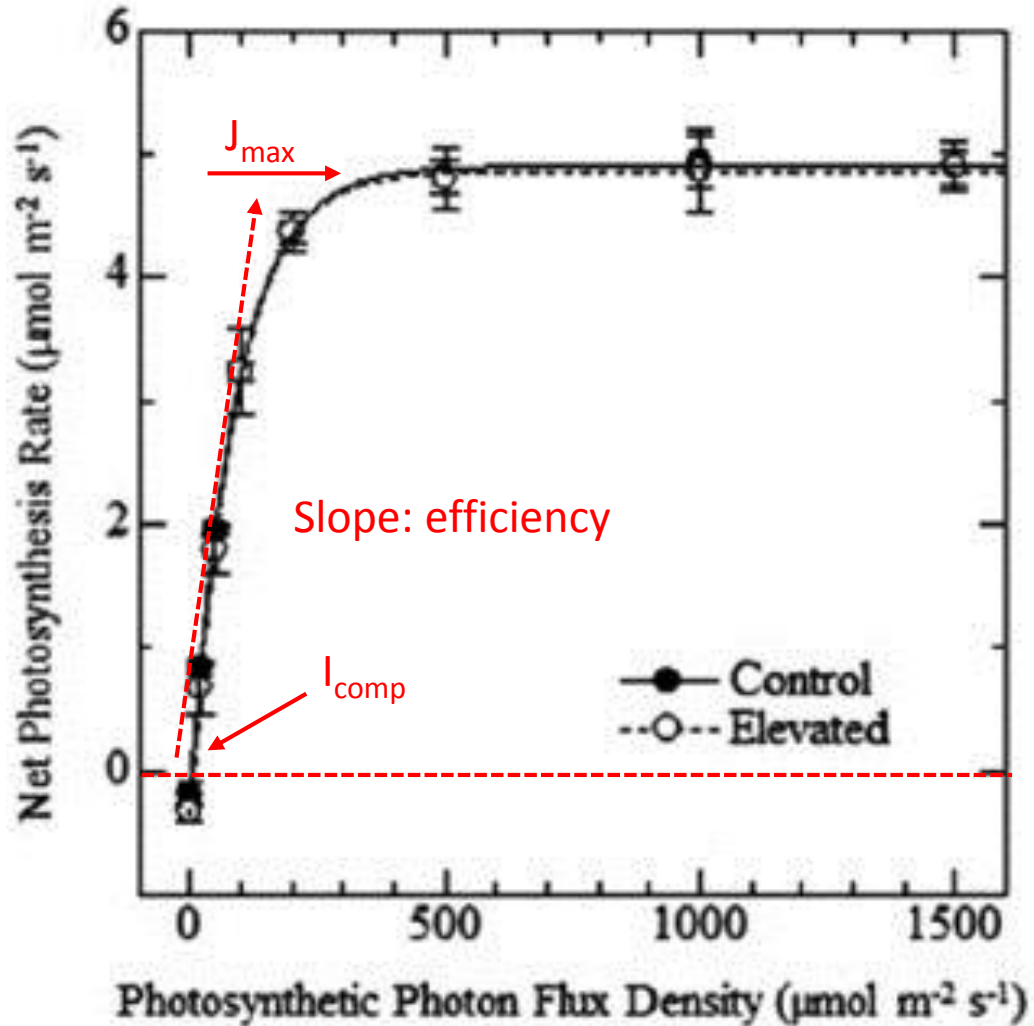
2.2.8 Water use efficiency (WUE) model

### Major variables and Symbols

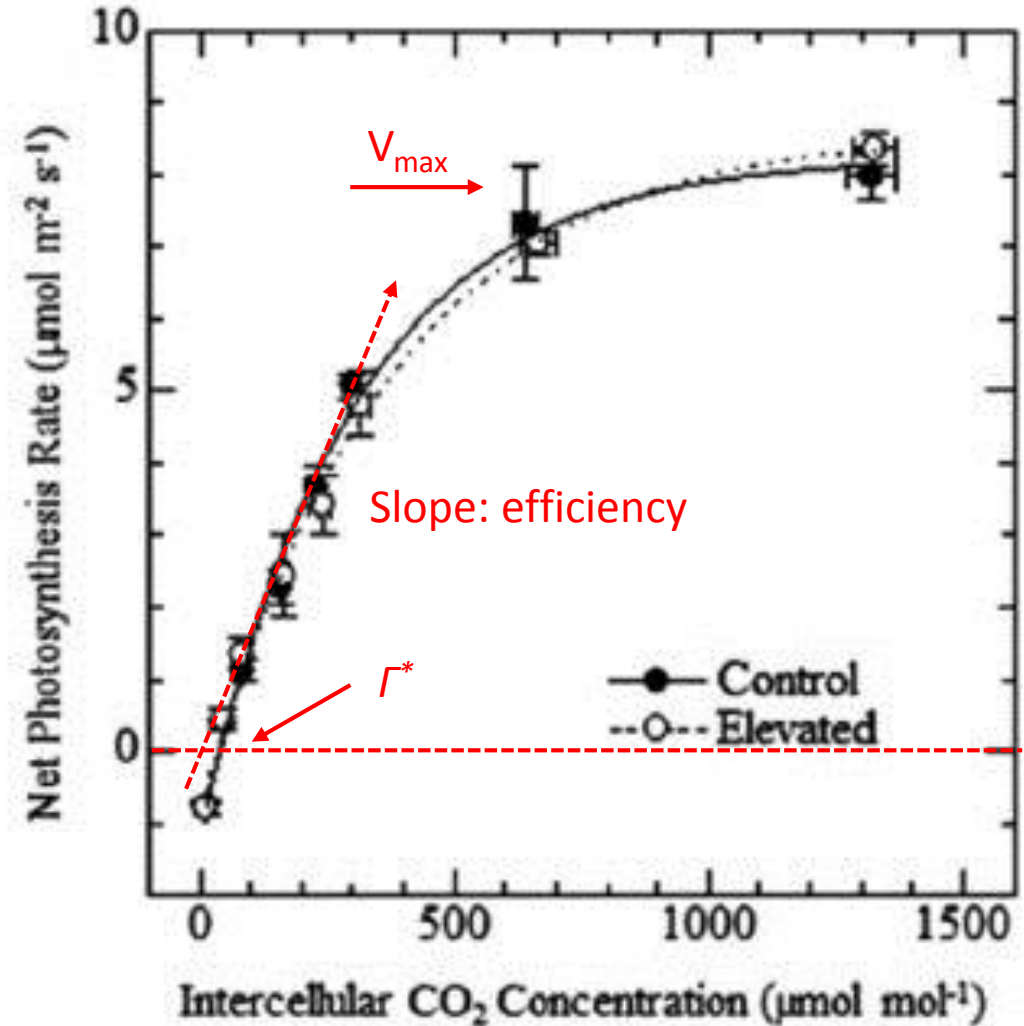
$P_n/A_n$ :	Photosynthesis rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
PAR (PPFD):	photosynthetically active radiation ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
VPD:	vapor pressure deficit (kPa)
$I_o$ or $I_{comp}$	light compensation point ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$\Gamma^*$ :	$\text{CO}_2$ compensation point (ppm)
$P_{max}/A_{max}$ :	maximum $P_n$ or $A$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$V_{max}$ :	maximum $P_n$ under $\text{CO}_2$ limited ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$J_{max}$ :	maximum $P_n$ under light limited ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
$g_s$ :	Stomata conductance ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )



# 1. Light response curve



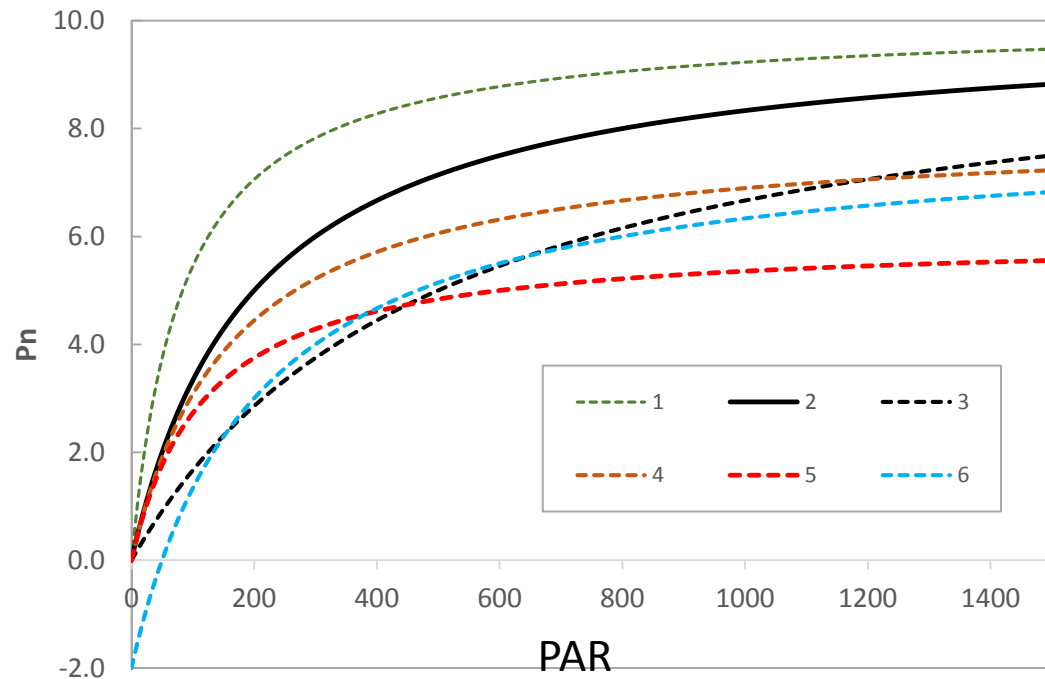
# 2. A-C<sub>i</sub> curve



## 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	$\alpha$	$P_m$	$R_d$
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

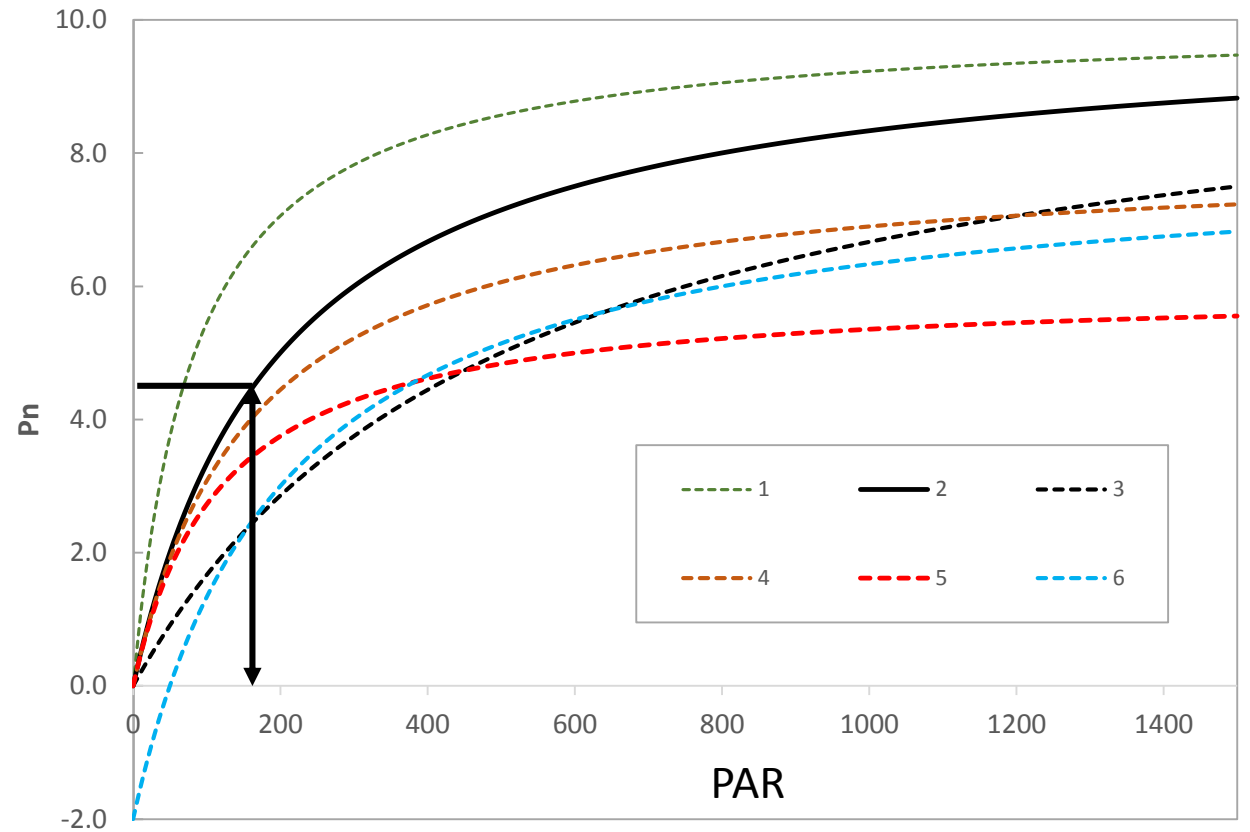
MM model with Respiration ( $R_d$ )

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

## 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 ( $\beta$ ) into a non-rectangular hyperbolic model

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

$$Y = a + b \cdot x + c \cdot x^2$$

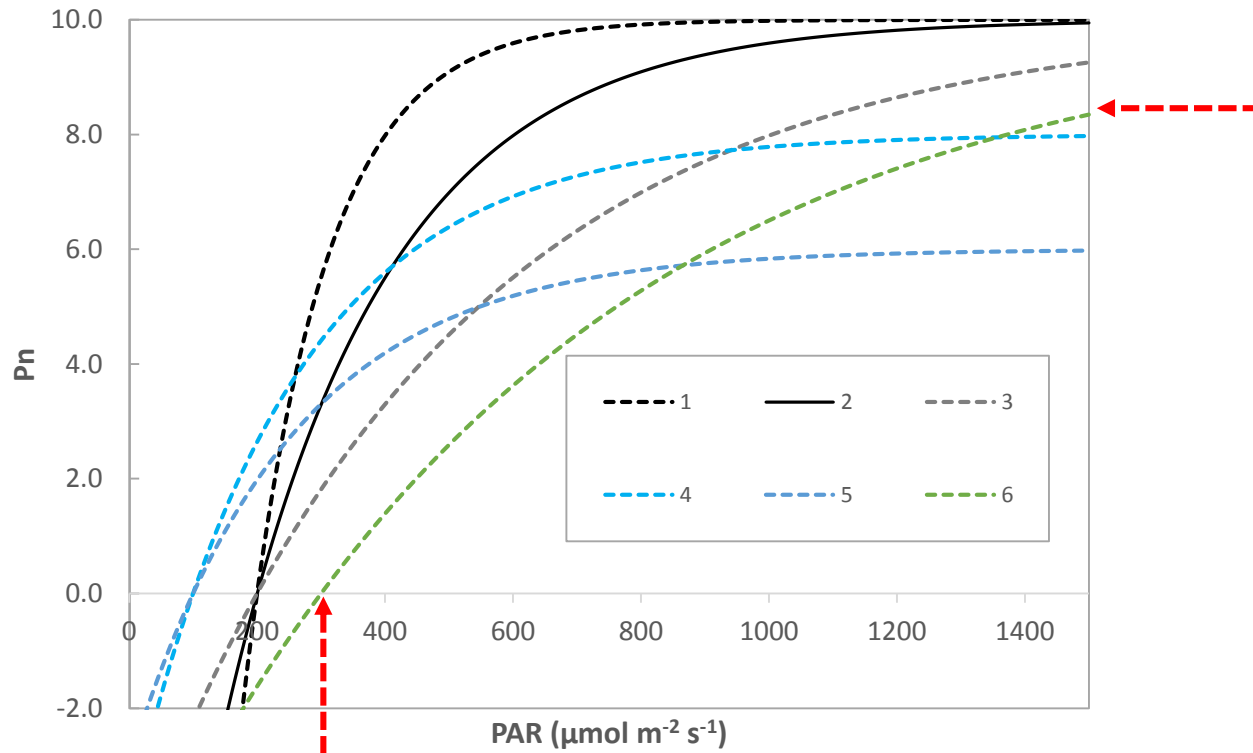
This model is virtually the same as Eq. 2.1 when  $\beta = 0$ . The value of  $\beta$  should be less than 1 for simulations.

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

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



Line	$\alpha$	$P_m$	$I_{comp}$
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 ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )

### 2.2.3 Farquhar's model

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

$A_c$  as a function of intercellular  $\text{CO}_2$  concentration is described by FvCB equation:

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

$V_{max}$  is the maximum activity of Rubisco

$c_i$  is the intercellular  $\text{CO}_2$  concentration ( $\mu\text{mol mol}^{-1}$ ),

$\Gamma^*$  is the  $\text{CO}_2$  compensation point in the absence of day respiration ( $R_d$ ),

$K_c$  is the Michaelis-Menten constant of Rubisco for  $\text{CO}_2$ ,

$O_i$  is the oxygen ( $\text{O}_2$ ) concentration in the atmosphere ( $209 \text{ mol mol}^{-1}$ ),

$K_o$  is the Michaelis-Menten constant of Rubisco for  $\text{O}_2$ .

### 2.2.3 Farquhar's model

$\Gamma^*$  is calculated as:

$$\Gamma^* = \frac{0.5 \cdot O_i}{2600 \cdot 0.57 Q^{10}}$$

$K_c$  for  $\text{CO}_2$  is calculated as:

$$K_c = 30 \cdot 2.1^{Q^{10}}$$

$K_o$  for  $\text{O}_2$  is calculated as:

$$K_c = 30000 \cdot 1.2^{Q^{10}}$$

### 2.2.3 Farquhar's model

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

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

$j$  is the electron transport rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and varies with absorbed photosynthetically active radiation ( $aPAR$ ).

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

$$A_p = 3 \cdot T_p$$

$T_p$  ( $\mu\text{mol m}^{-2}$ ) 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:  $A_n = \text{minimum}(A_c, A_j, A_p)$

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

$V_{max}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),

$J_{max}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),

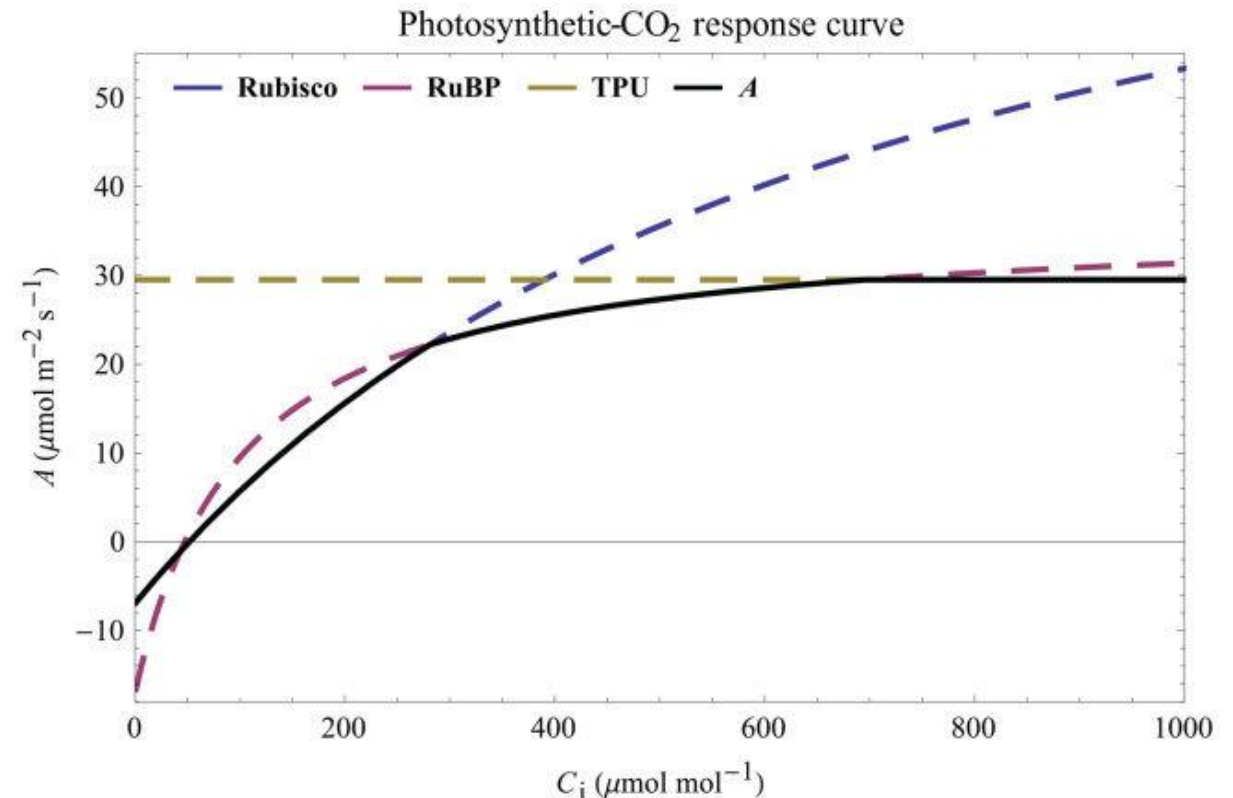
$T_p$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )

$R_d$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )

Web Sources for A models

<https://biocycle.atmos.colostate.edu/shiny/photosynthesis/>

<https://leafweb.org/>



[https://www.researchgate.net/publication/236199968\\_Modeling\\_C3\\_photosynthesis\\_from\\_the\\_chloroplast\\_to\\_the\\_ecosystem/figures?lo=1](https://www.researchgate.net/publication/236199968_Modeling_C3_photosynthesis_from_the_chloroplast_to_the_ecosystem/figures?lo=1)

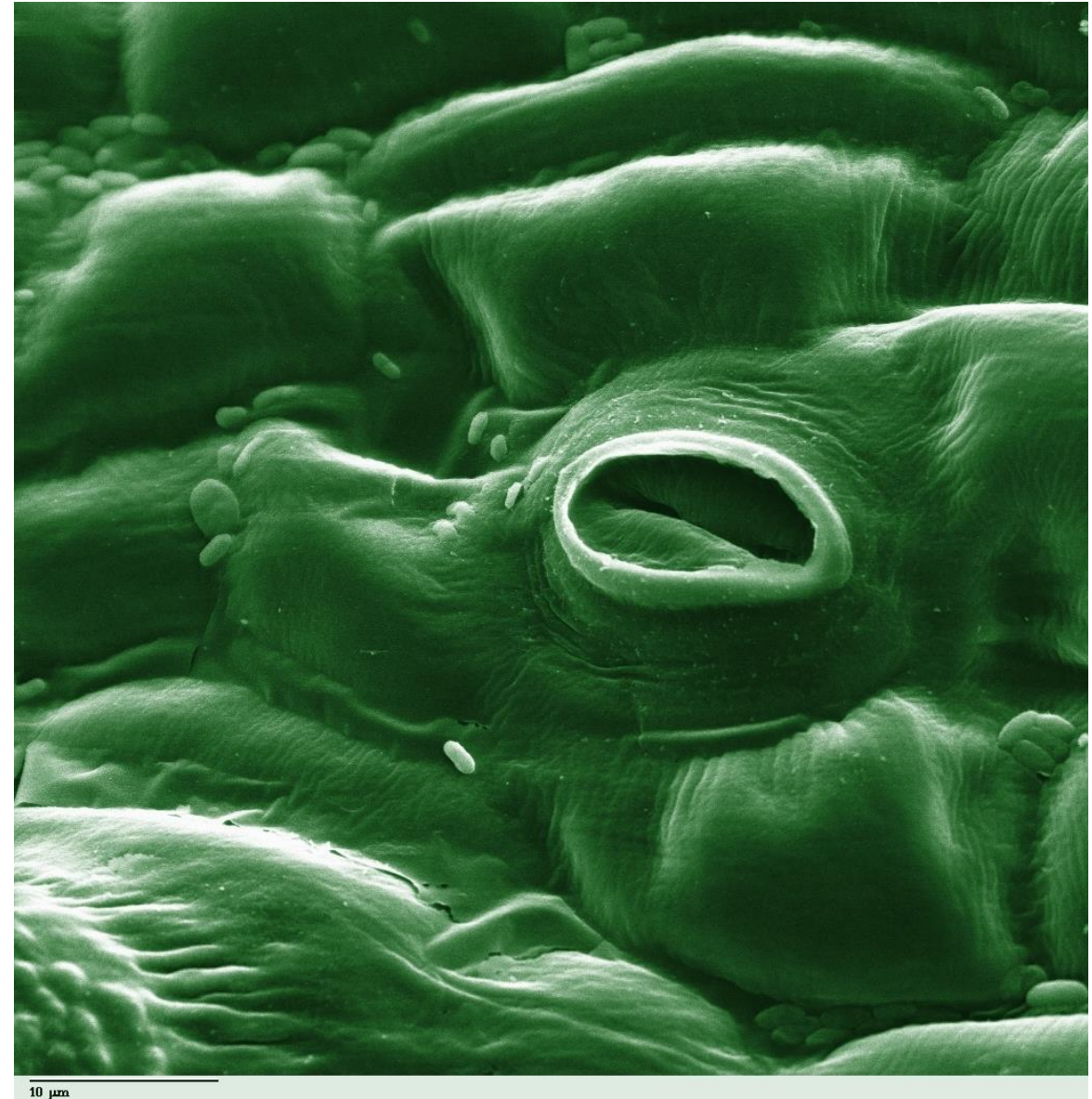
## 2.2.4 Photosynthesis based on stomatal conductance ( $g_s$ )

- The diffusion rate is called stomatal conductance ( $g_s$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), which is proportional to the photosynthesis rate ( $A_n$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).
- This linear relationship is modulated by leaf surface  $\text{CO}_2$  and  $\text{H}_2\text{O}$  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,
- $c_s$  ( $\mu\text{mol mol}^{-1}$ ) is the  $\text{CO}_2$  concentration of leaf surface,
- $K$  is the slope constant of the model that represents the composite sensitivity of  $g_s$  to  $\text{CO}_2$  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<sup>-2</sup> s<sup>-1</sup>). 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:

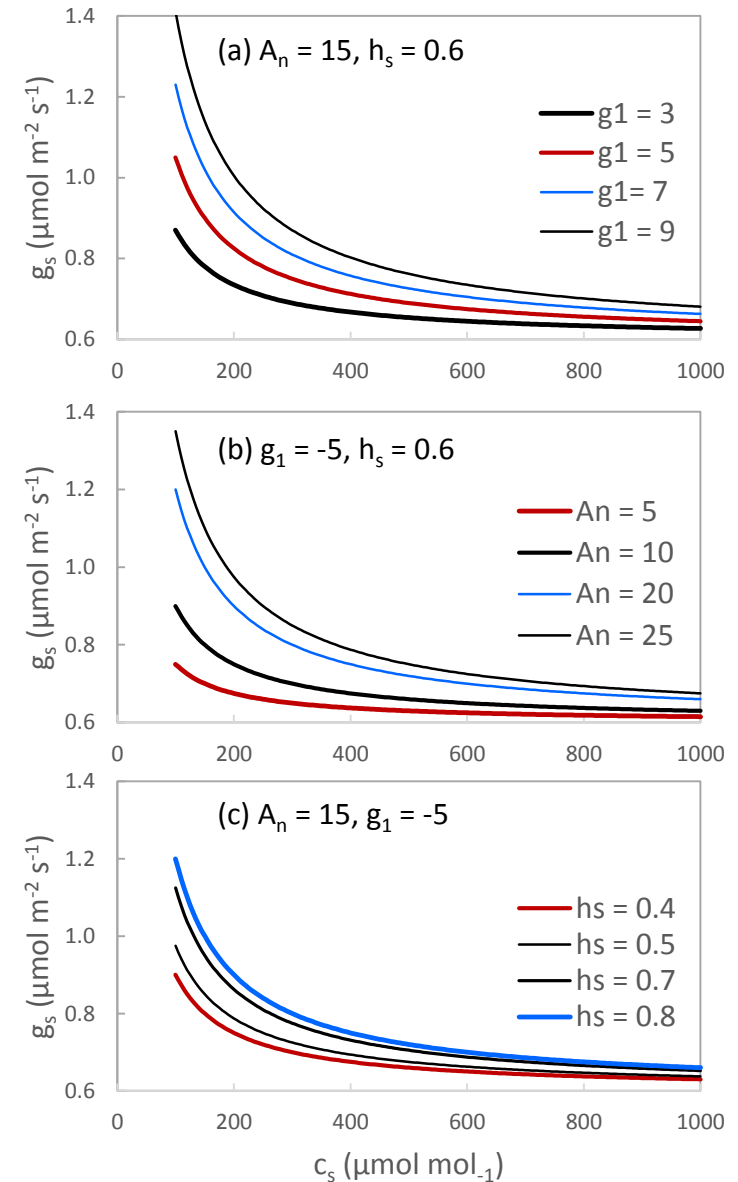
$$g_s = g_0 + \frac{a_1 \cdot A_n}{(c_s - \Gamma) \left(1 + \frac{D_s}{D_0}\right)}$$

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

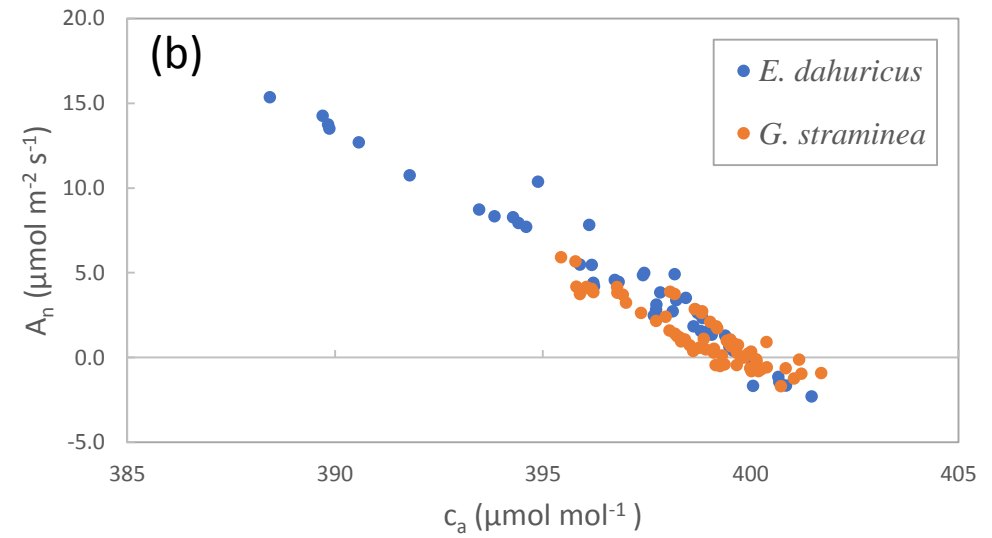
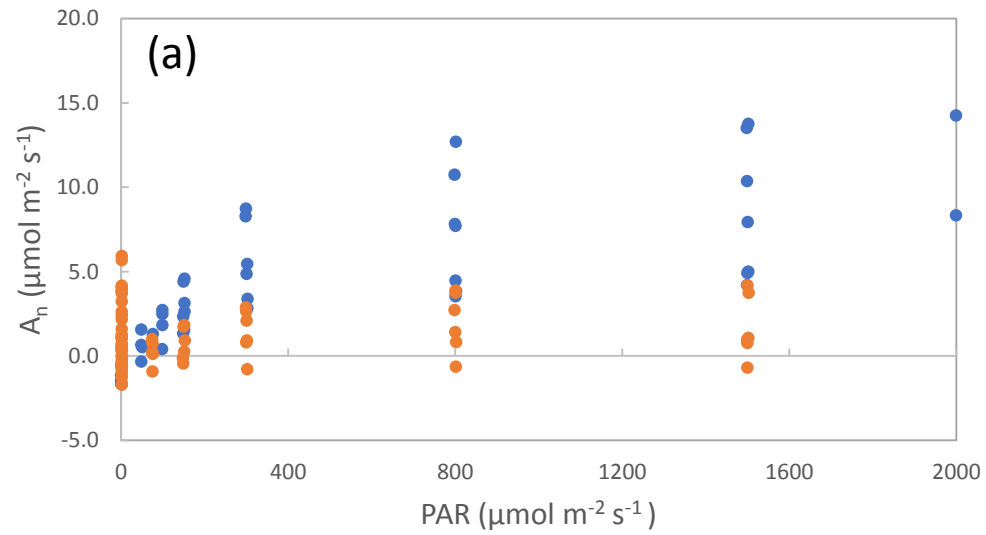
Lloyd (1991) proposed that  $g_s$  is dependent of  $\sqrt{D}$ . Medlyn *et al.* (2011) further emphasized the importance of  $g_1$  in the Ball-Berry model because of its sensitivity to environmental changes (*e.g.*, temperature, soil water and nutrients). They also agreed with Leuning *et al.* (1995)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

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

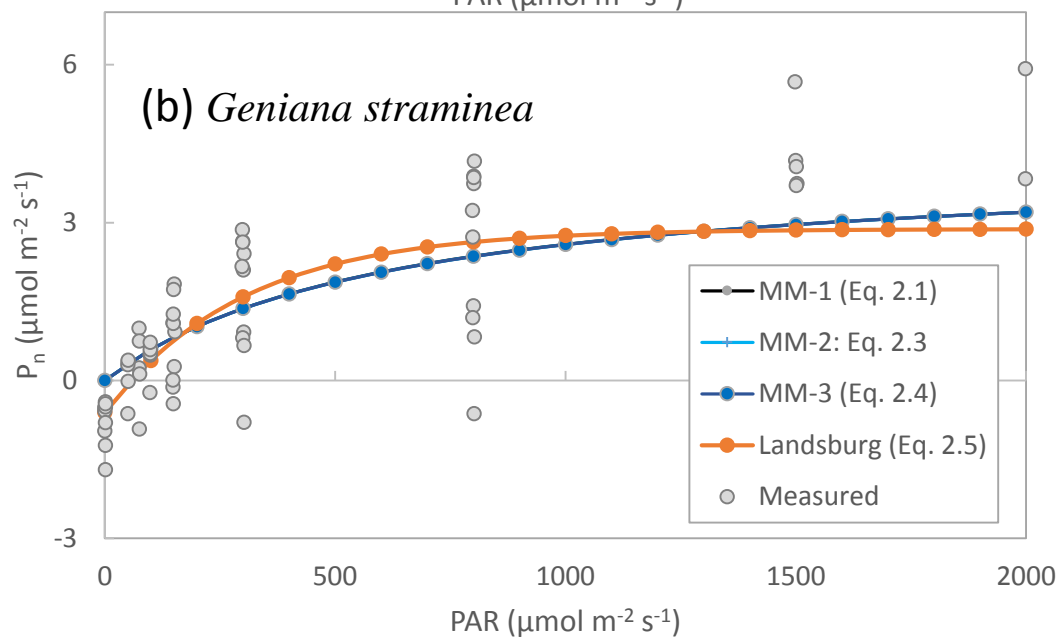
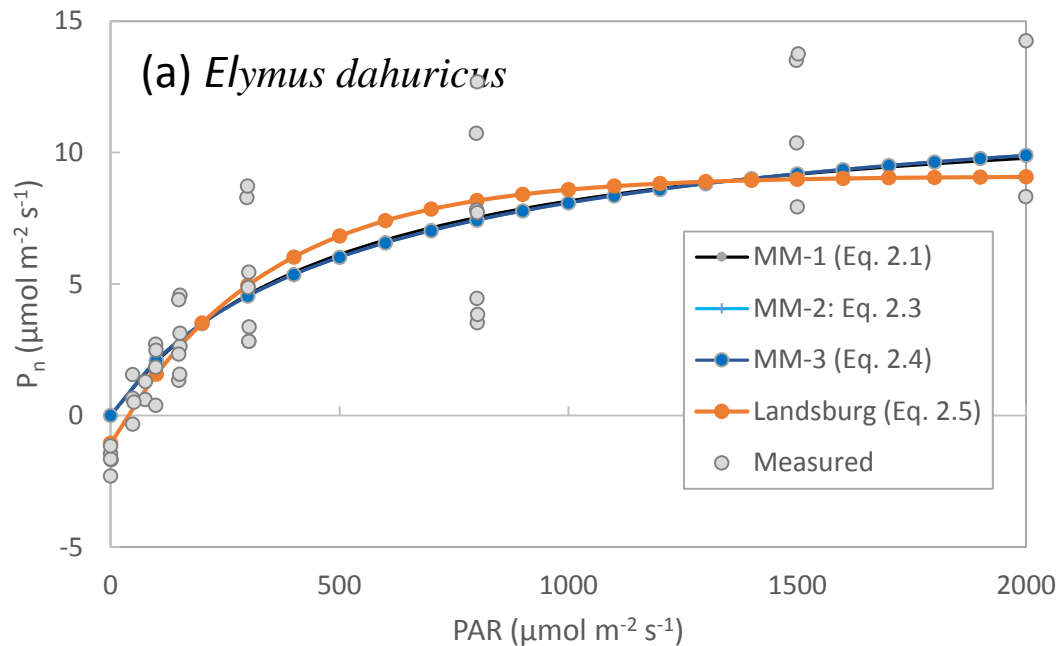
**Figure 2-4.** Simulations of stomatal conductance ( $g_s$ ) with different sets of parameters (Eq. 2.13). Other curves can be generated by altering parameters in **S2-2**



**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).

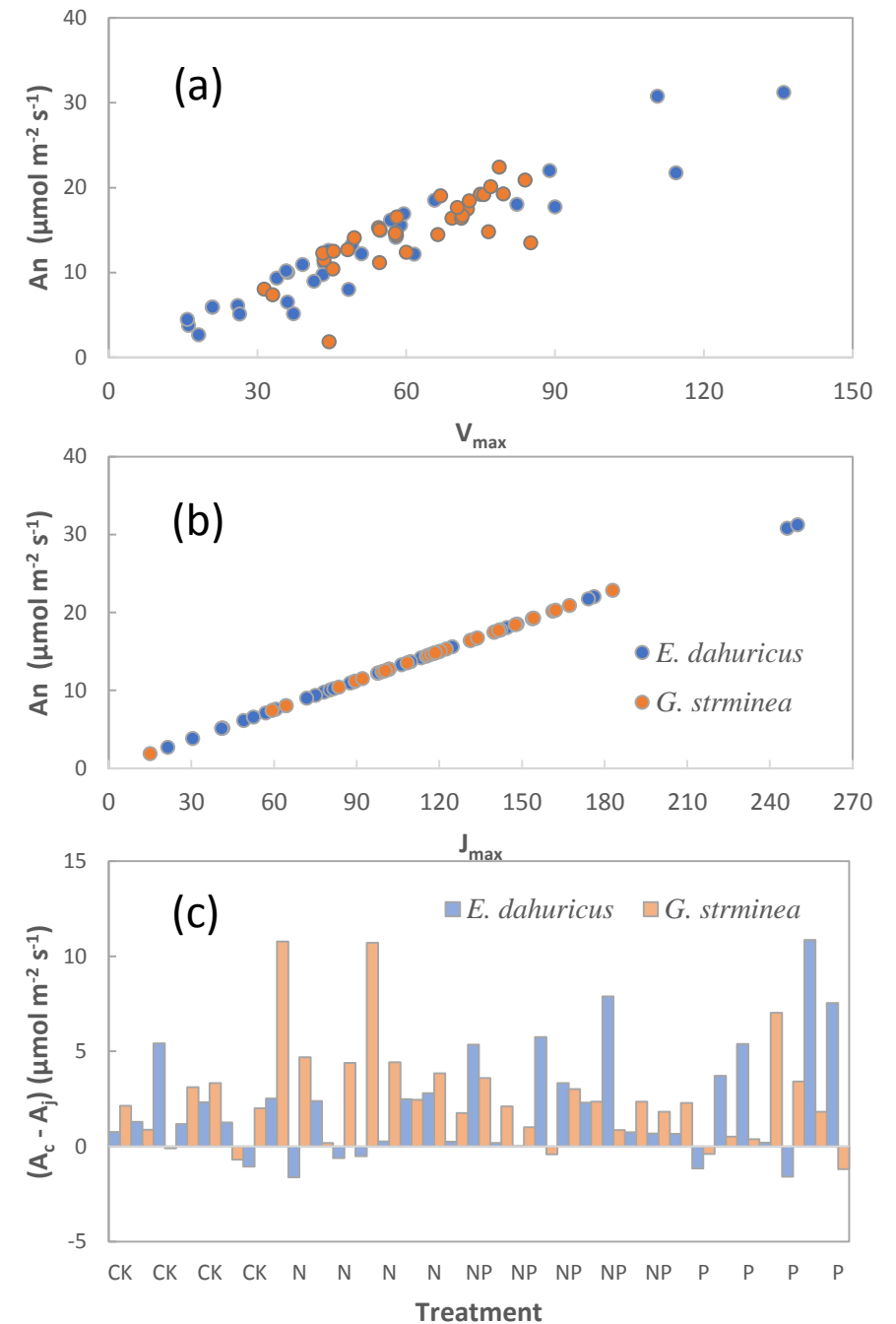


	MM-1	MM-2	MM-3	Landsberg
$\alpha$	0.024	0.027	0.027	-0.003
$\beta$		-0.421	-0.421	9.102
$I_{\text{comp}}$				36.83
$P_m$	12.224	13.108	13.108	
$r^2$	0.667	0.668	0.668	0.664
MSE	6.844	6.841	6.841	6.785

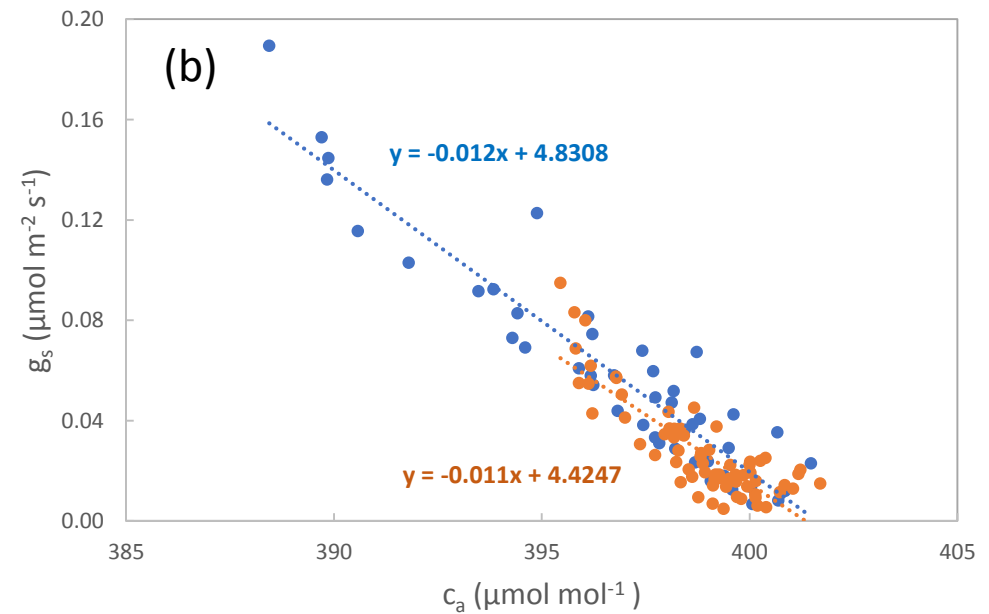
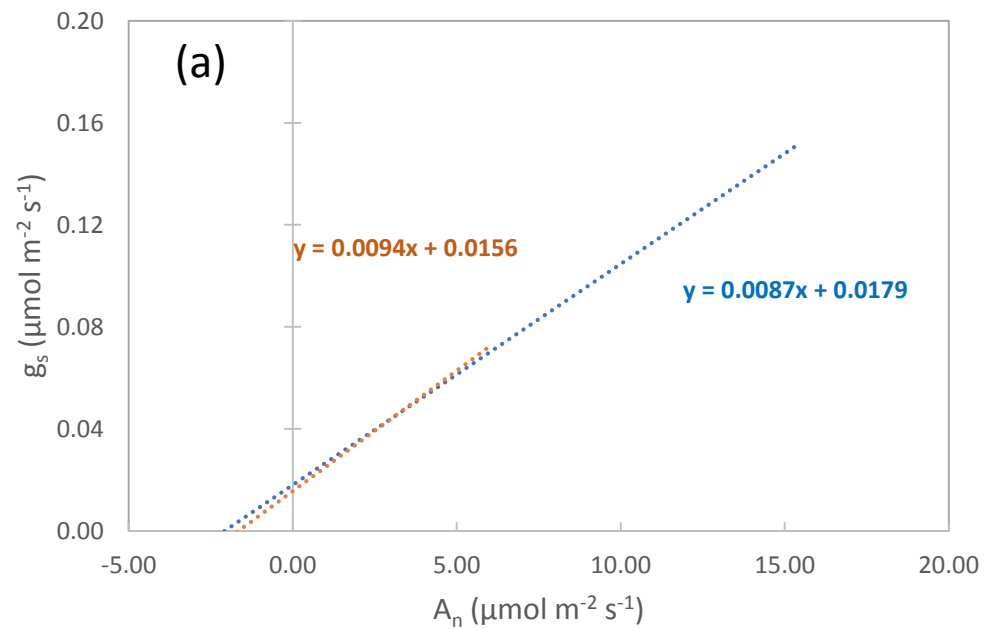
	MM-1	MM-2	MM-3	Landsberg
$\alpha$	0.007	0.007	0.007	-0.003
$\beta$		4.213	4.215	2.879
$I_{\text{comp}}$				58.207
$P_m$	4.189	-0.025	-0.026	
$r^2$	0.520	0.520	0.520	0.526
MSE	1.536	1.536	1.536	1.475



**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<sub>2</sub> 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

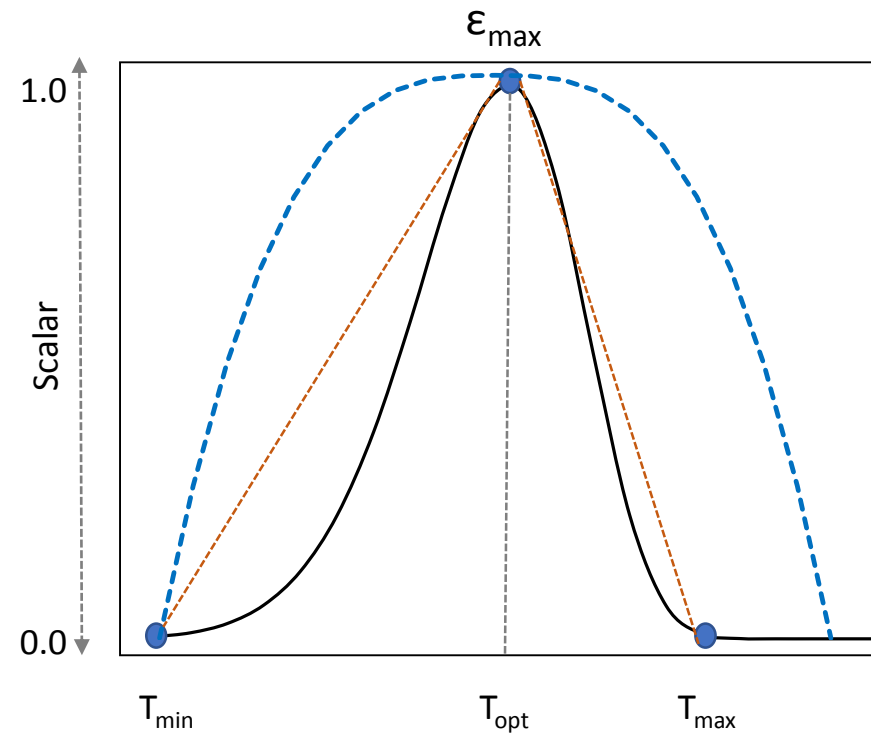
Ecosystem primary production ( $GPP$ , or  $NPP$ ), or canopy photosynthesis ( $P_n$ ), can be simply molded as a portion of  $PAR$  – light use efficiency ( $\epsilon$ ):

$$P_n = \epsilon \cdot Water$$

LUE model for estimating ecosystem primary production is simple, using  $aPAR$  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:

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

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



## *PnET model*

$P_{max}$  ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) 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:

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

## Water use efficiency (WUE)

Assuming CO<sub>2</sub> uptake and H<sub>2</sub>O loss are coupled, *GPP* at ecosystem can be modeled 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:

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

## 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 associated with the textbook

- ~ 30 different files on dozens of models

## 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 ( $A_n$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) 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.

- Each file has multiple models

- ❖ Lightresponse

- ❖ RModel1





## Q&A from the Class (5-min break)

- Get your laptop started and Python compiler fired up!
- A short grad/undergrad course will be organized at the East China Normal University during Oct-Dec, 2021. I will spend 7-10 hours with detailed uses of the models. Contact Dr. Jianyang Xia for details ([jyxia@des.ecnu.edu.cn](mailto:jyxia@des.ecnu.edu.cn))

# In-class practices of selected models

1. Calculating VPD from Ta and RH (Chapter 1: [Ta\\_h\\_VPD.xlsx](#)) (*additional versions in R, Python, SAS are available pending on request*)
2. Calculating sun rise/set time and solar elevation (Chapter 1: [Solar.py](#)) (*different versions can be requested*)
3. (Light response curves (Chapter 2: [LightResponse.xlsx](#)))
4. Non-linear models (Chapter 3: [R3-10.Py](#))
5. Respiration models (Chapter 3: [Rmodel\\_2.xlsx](#))
6. ET models (Chapter 4: [ETmodels.xlsx](#))
7. Calculating global warming potentials (Chapter 5: [GWP\\_Model.xlsx](#)) (*a new version in Python is available pending on request*)

# Contact Information

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