

# Mechanisms Controlling the Temperature Response of C<sub>4</sub> Photosynthesis

Rowan Sage

Department of Ecology and Evolutionary  
Biology, University of Toronto, Toronto ON M5S3B2

# **C<sub>4</sub> Photosynthesis Supercharges Biomass Production**

**Maize C<sub>4</sub>**

**Grain Yield = 13.9 t ha<sup>-1</sup>**

**44 DAG**

**Echinochloa C<sub>4</sub>**

**42 DAT**

**Rice C<sub>3</sub>**

**Grain Yield = 8.3 t ha<sup>-1</sup>**

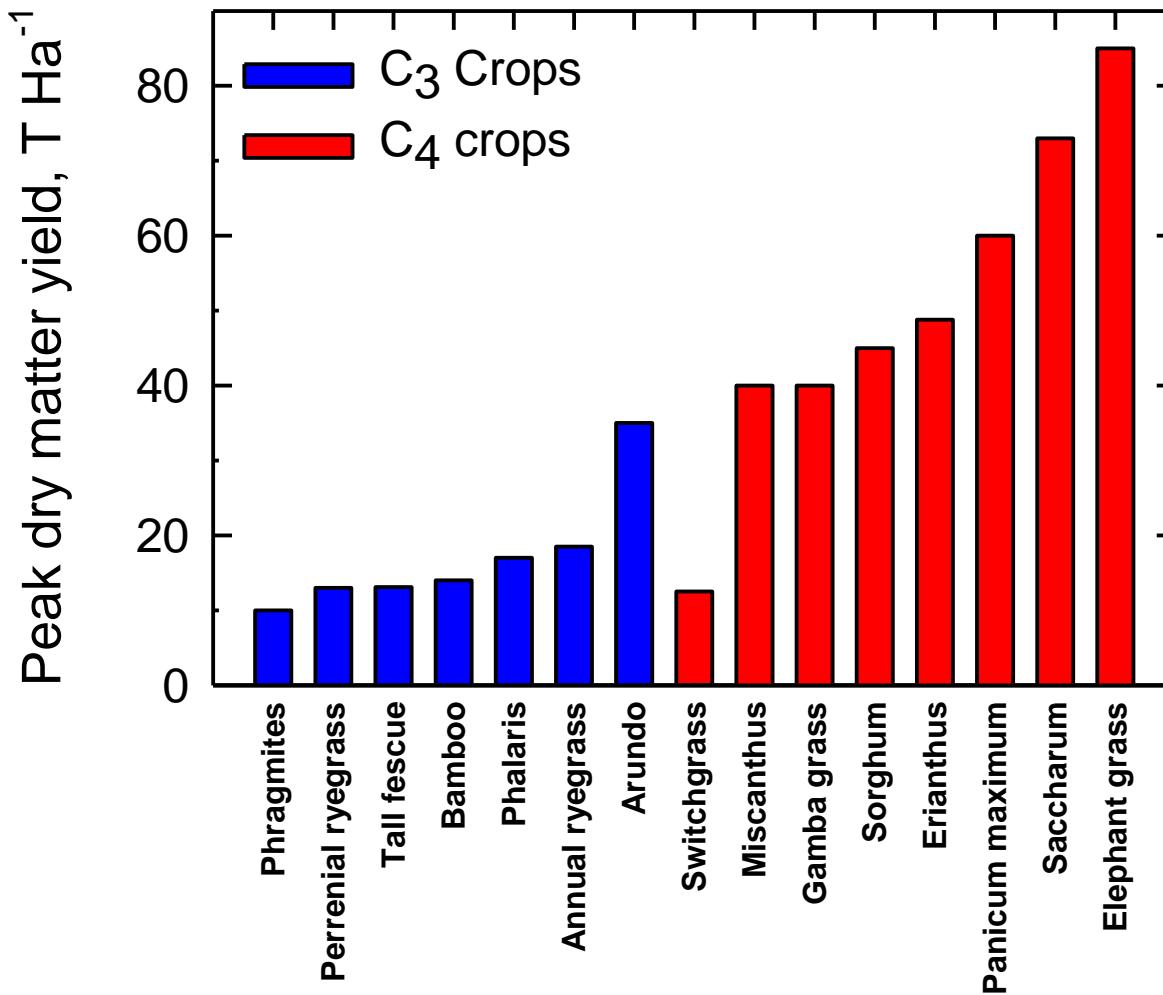
**42 DAT**

Slide courtesy of John Sheehy, International Rice Research Institute

DAG = Days after germination  
DAT = Days after transplanting

# Maximum Dry Matter Yields Reported for Biofuel Crops

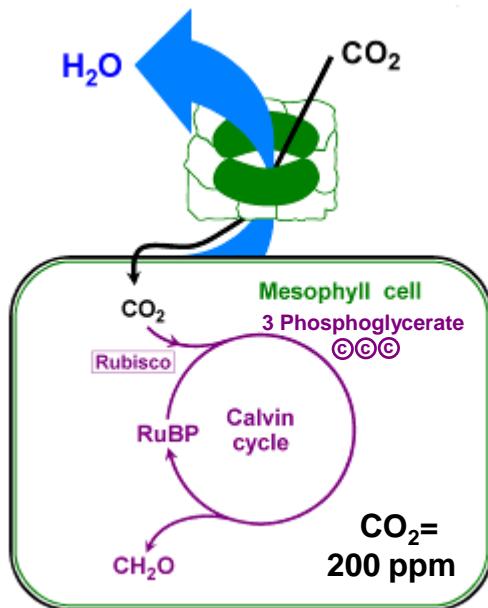
from El Bassam (1997) *Energy Plant Species*



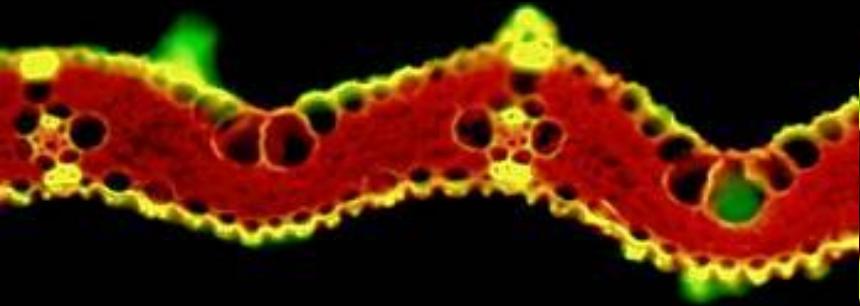
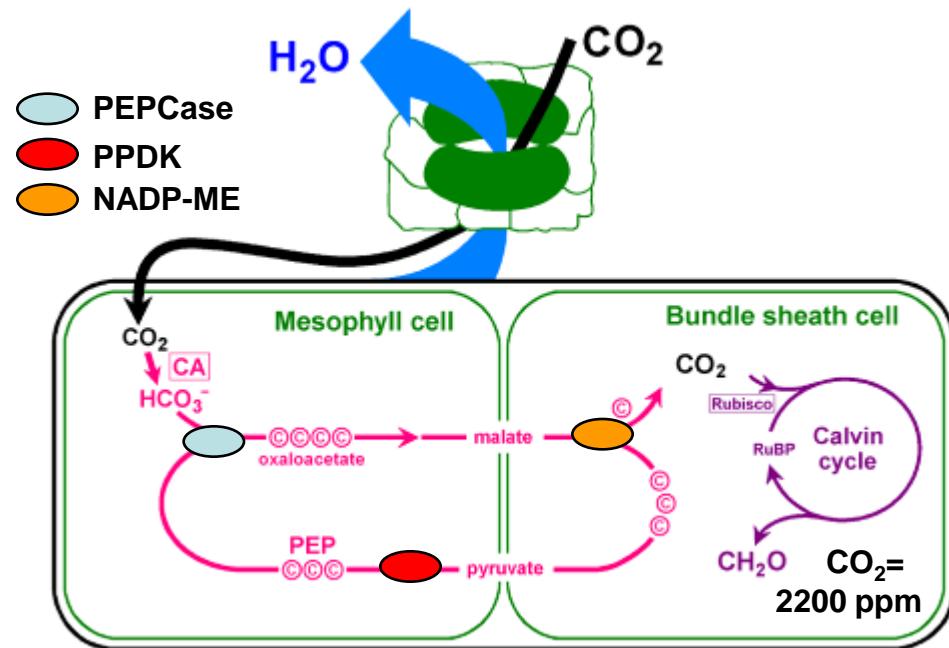
# C<sub>4</sub> Supercharges Photosynthesis Using A Two Compartment CO<sub>2</sub> Concentrating Mechanism

Slide courtesy of John Sheehy, International Rice Research Institute

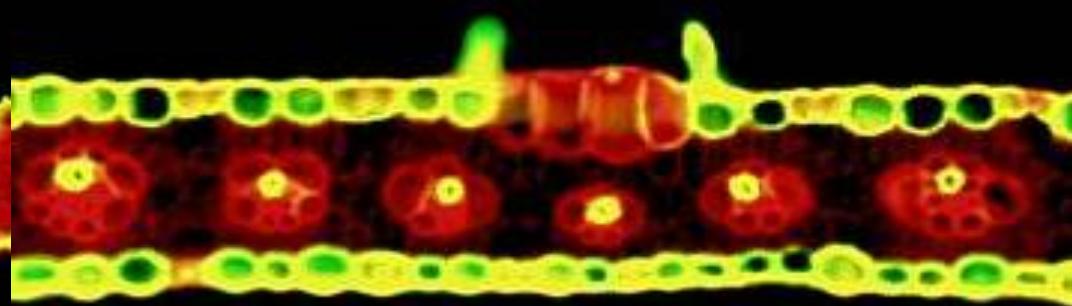
## C<sub>3</sub> Photosynthesis



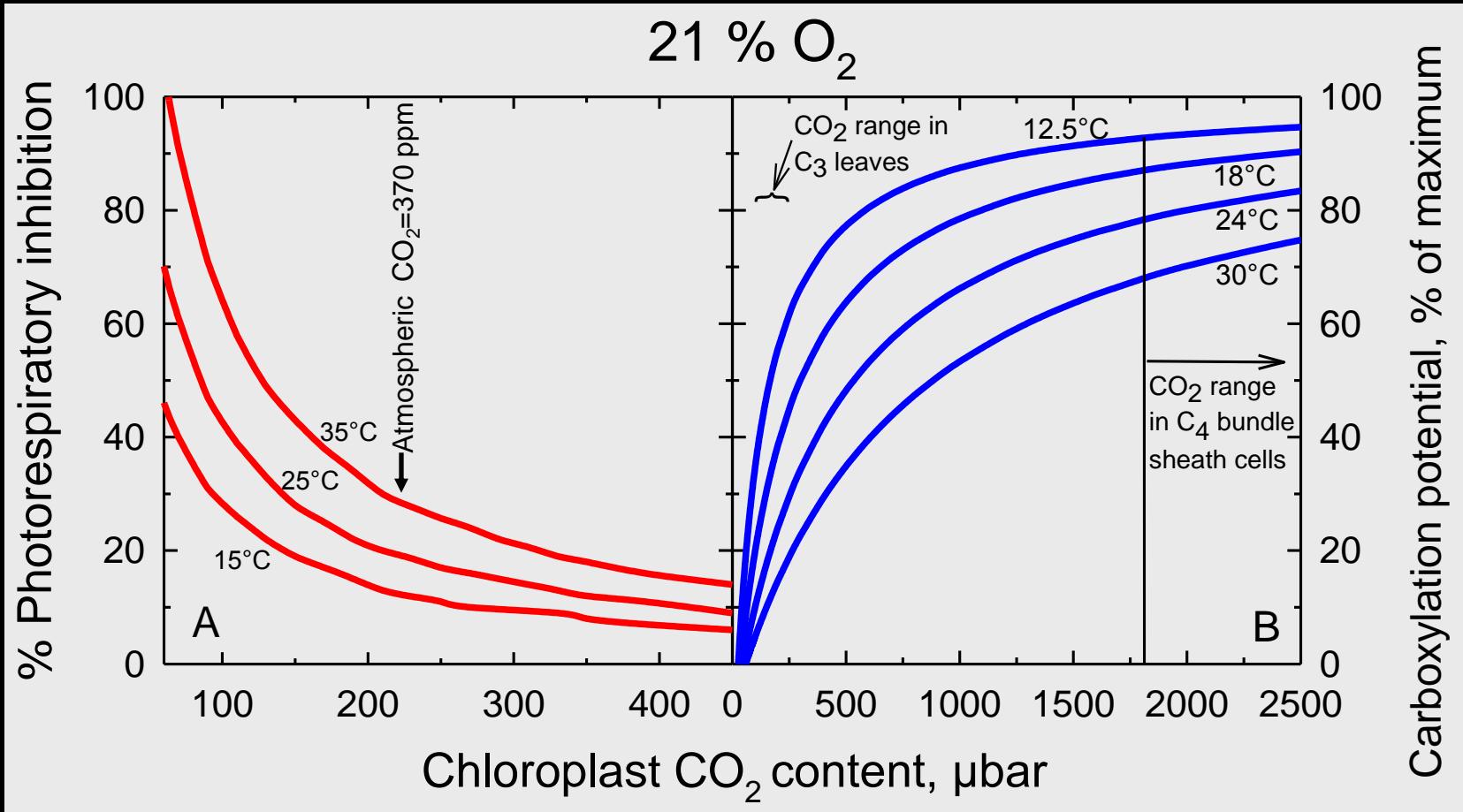
## C<sub>4</sub> Photosynthesis



C<sub>3</sub> Anatomy

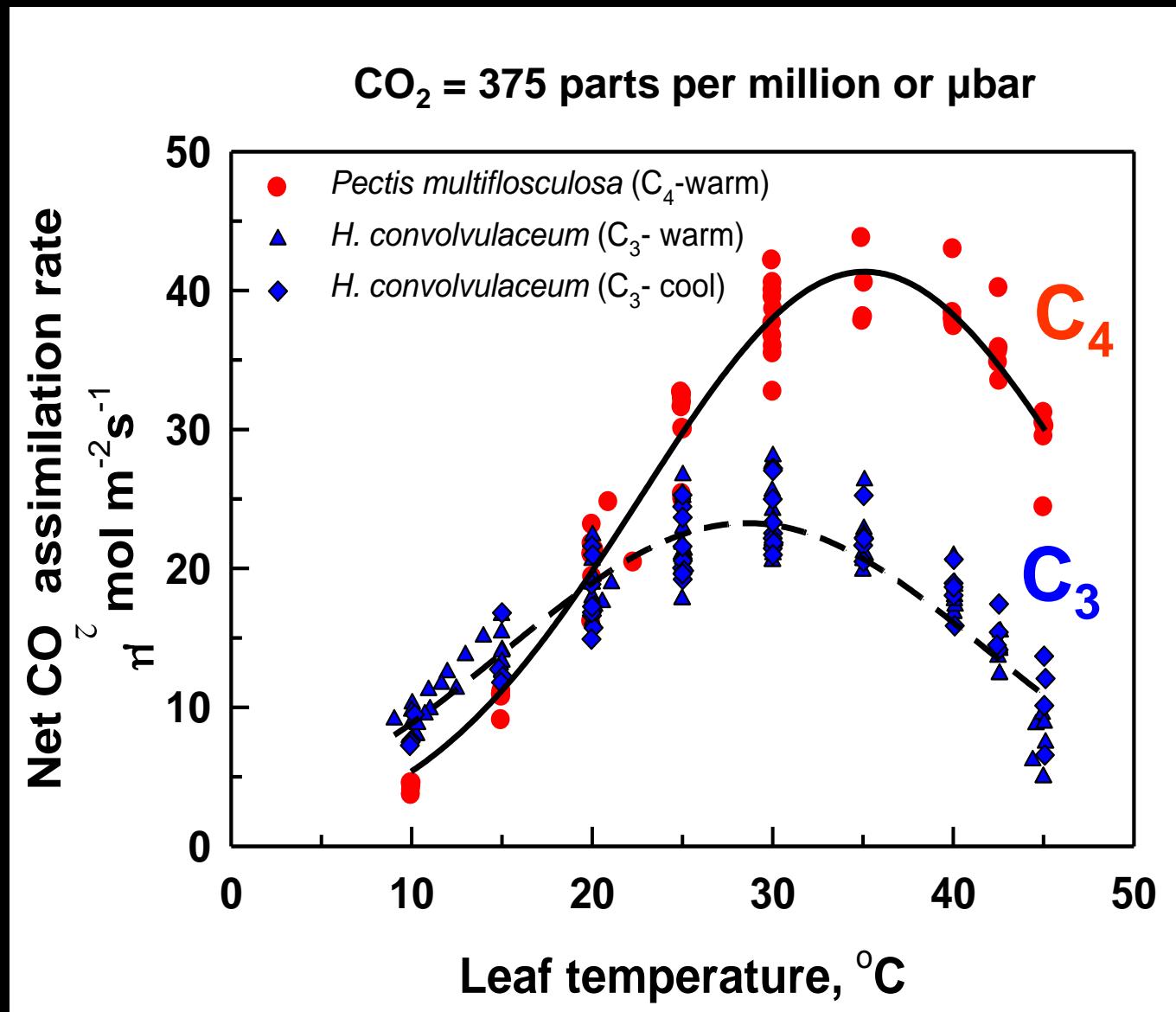


C<sub>4</sub> “Kranz” Anatomy

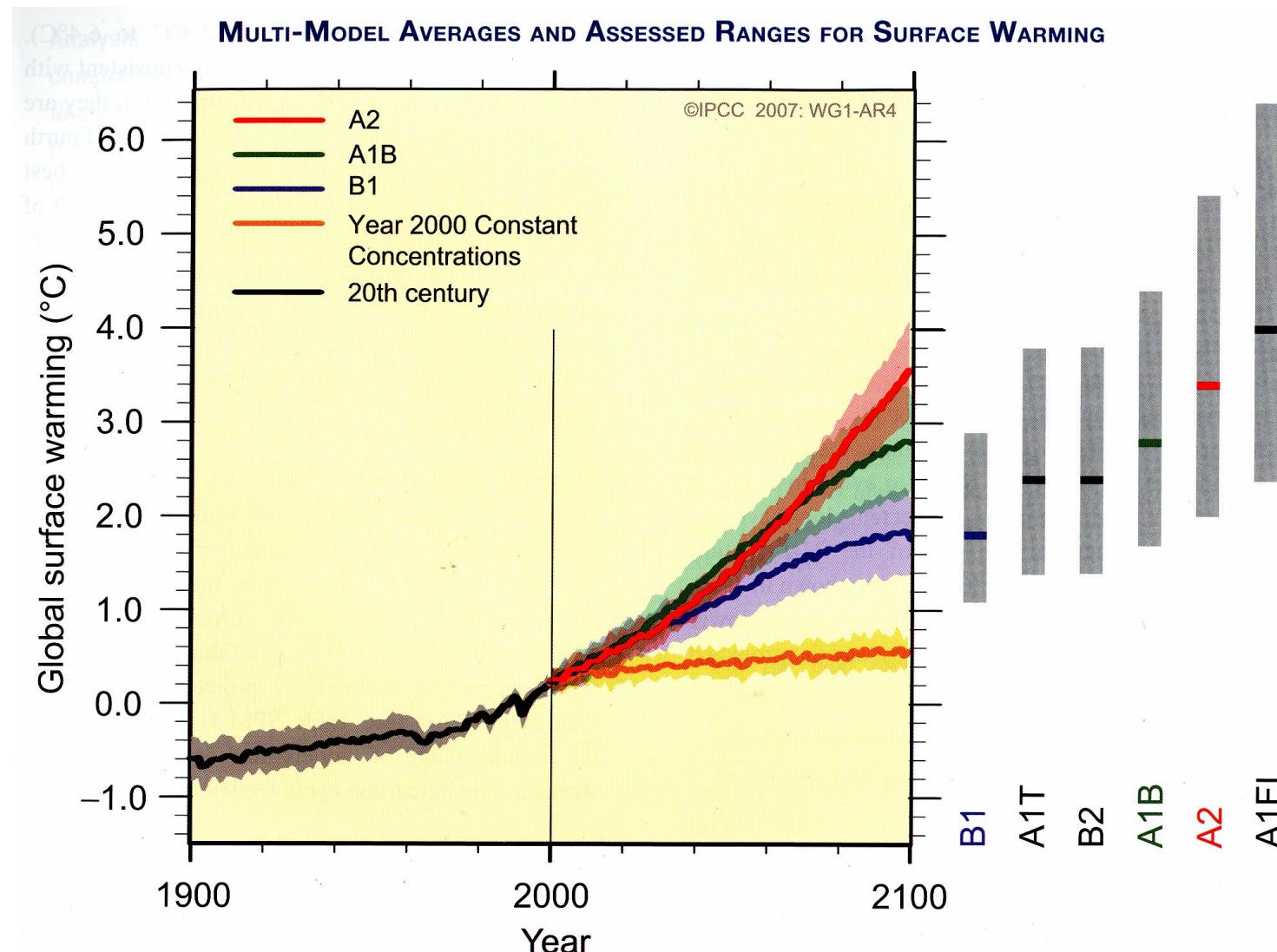


from Sage (2000) in *Redesigning Rice Photosynthesis to Increase Yield*.  
Sheehy, Mitchell and Hardy, eds. Elsevier.

# Typical C<sub>3</sub> and C<sub>4</sub> Photosynthetic Temperature Responses

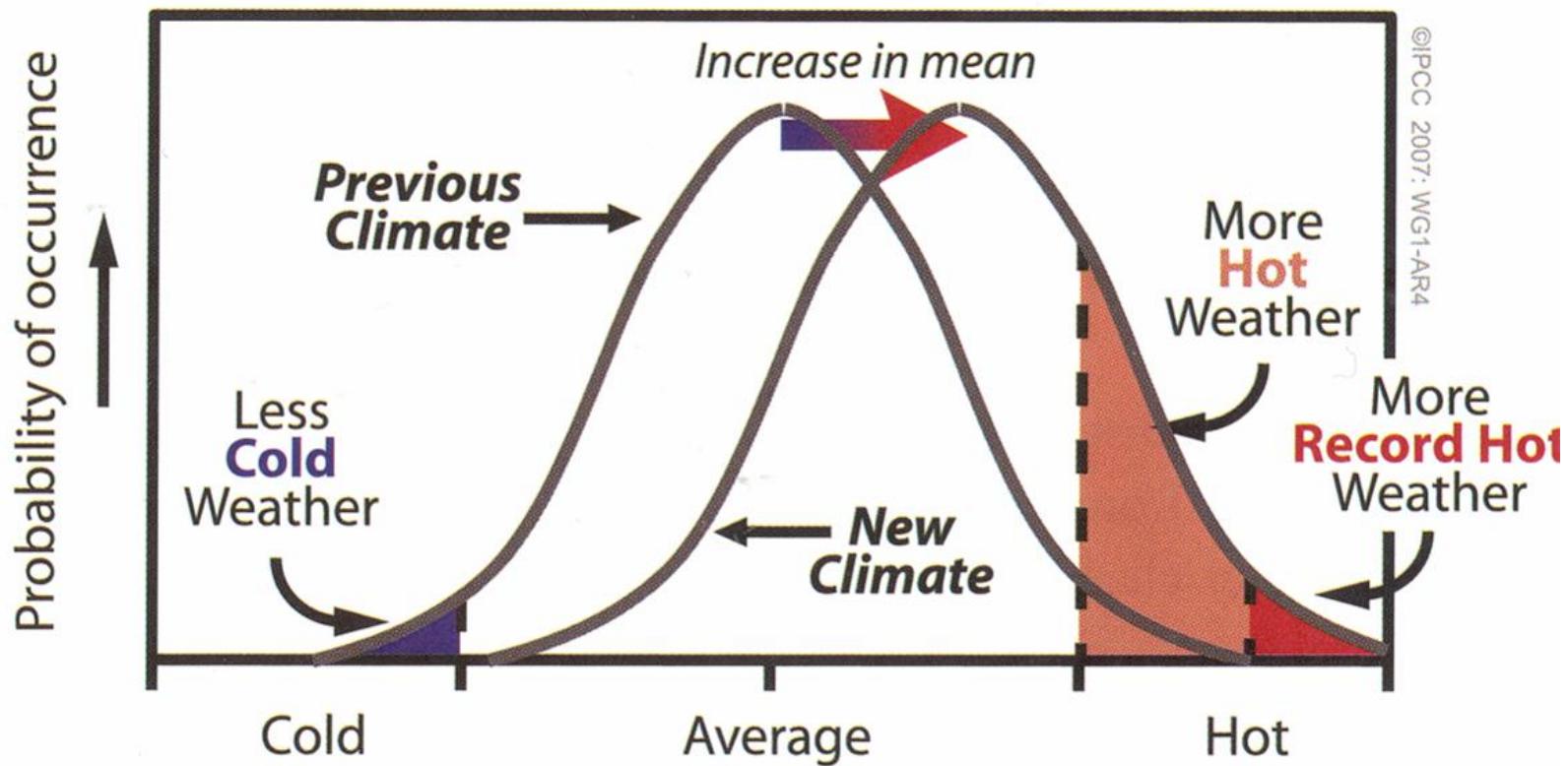


# Global Temperature Change and Modeled Predictions: 1900 to 2100



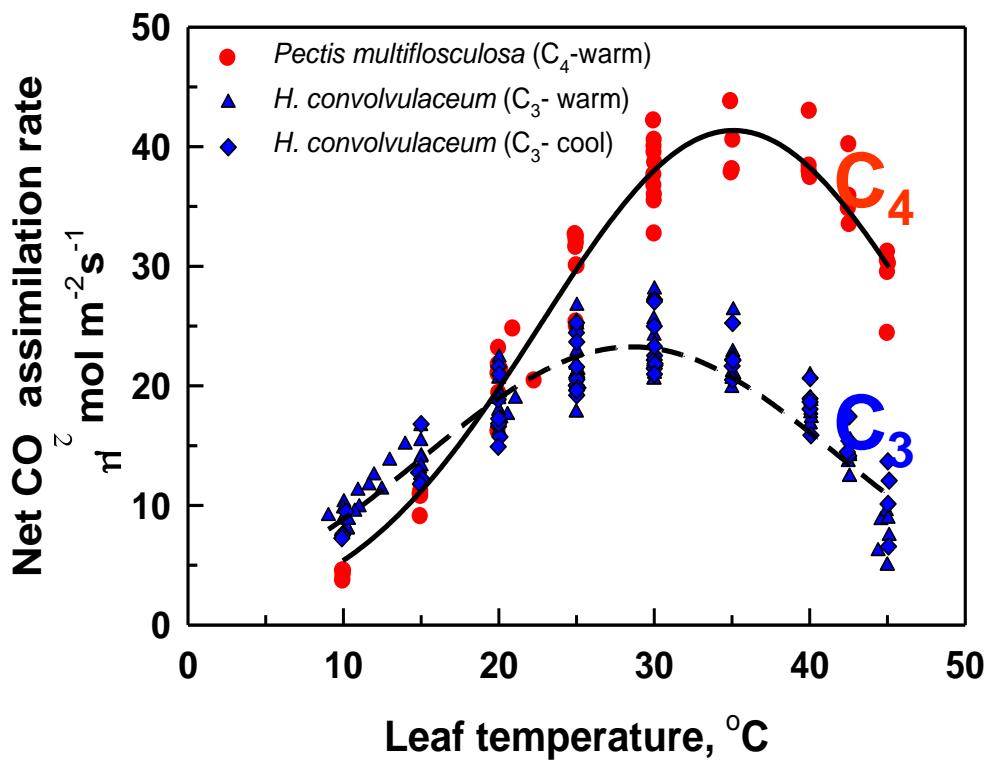
Source: Intergovernmental Panel on Climate Change (2007)  
Climate Change 2007: The Physical Basis. Cambridge Univ. Press

# A Schematic of How Warming Affects Climate



Source: Intergovernmental Panel on Climate Change (2007):  
Climate Change 2007: The Physical Basis. Cambridge Univ. Press

## Typical C<sub>3</sub> and C<sub>4</sub> Photosynthetic Temperature Responses



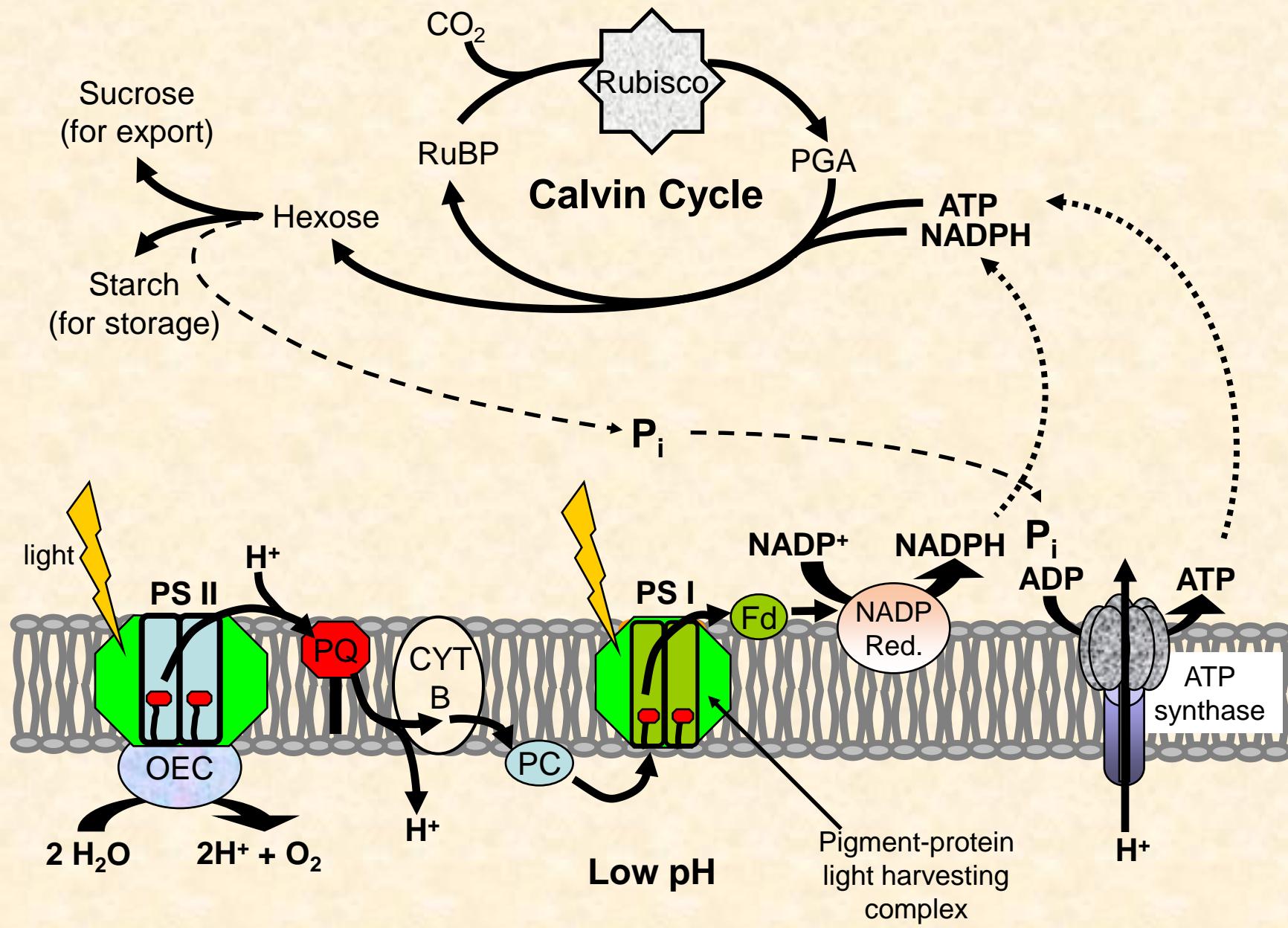
## Strategies to Improve the C<sub>4</sub> Response to Climate Warming

1. Exploit moderation of the cool season
2. Exploit warmer summers
3. Exploit warmer temperature and elevated CO<sub>2</sub> to enhance WUE and NUE.

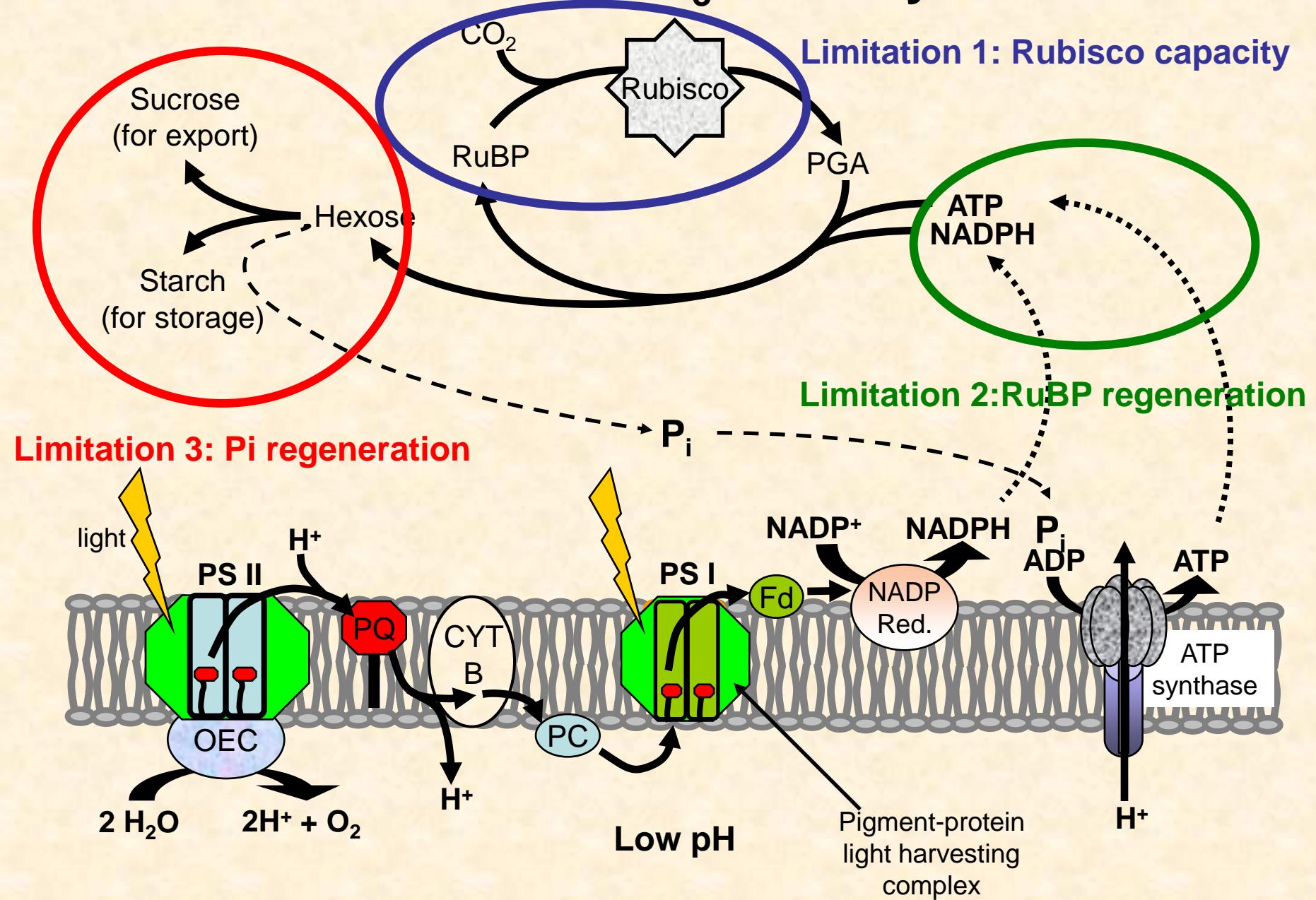
# Improving C<sub>4</sub> Photosynthesis

*To improve C<sub>4</sub> photosynthetic capacity in a crop plant, one should understand the biochemical processes that limit C<sub>4</sub> photosynthesis in the environment of interest.*

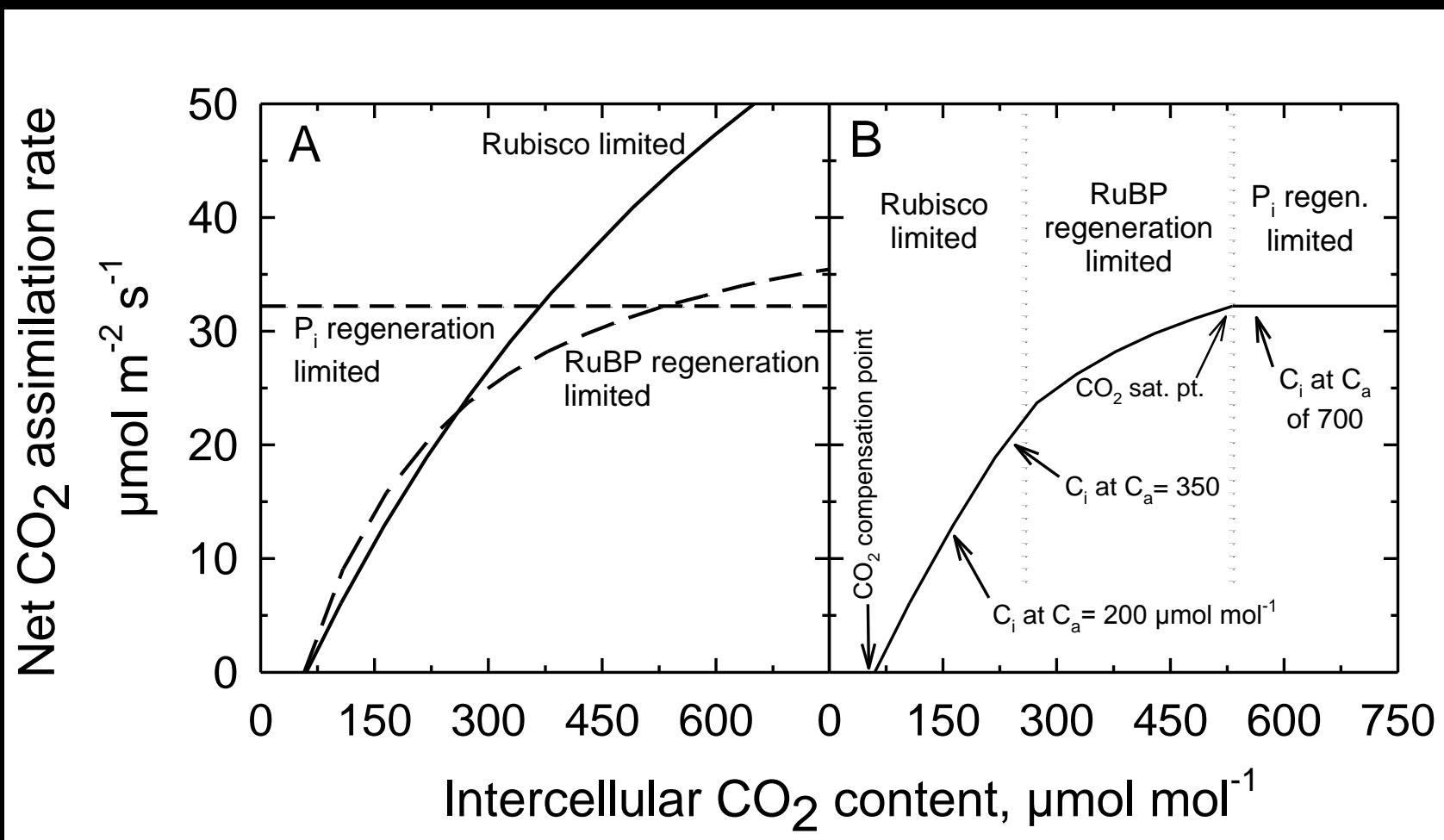
# A Schematic of C<sub>3</sub> Photosynthesis



# A Schematic of C<sub>3</sub> Photosynthesis

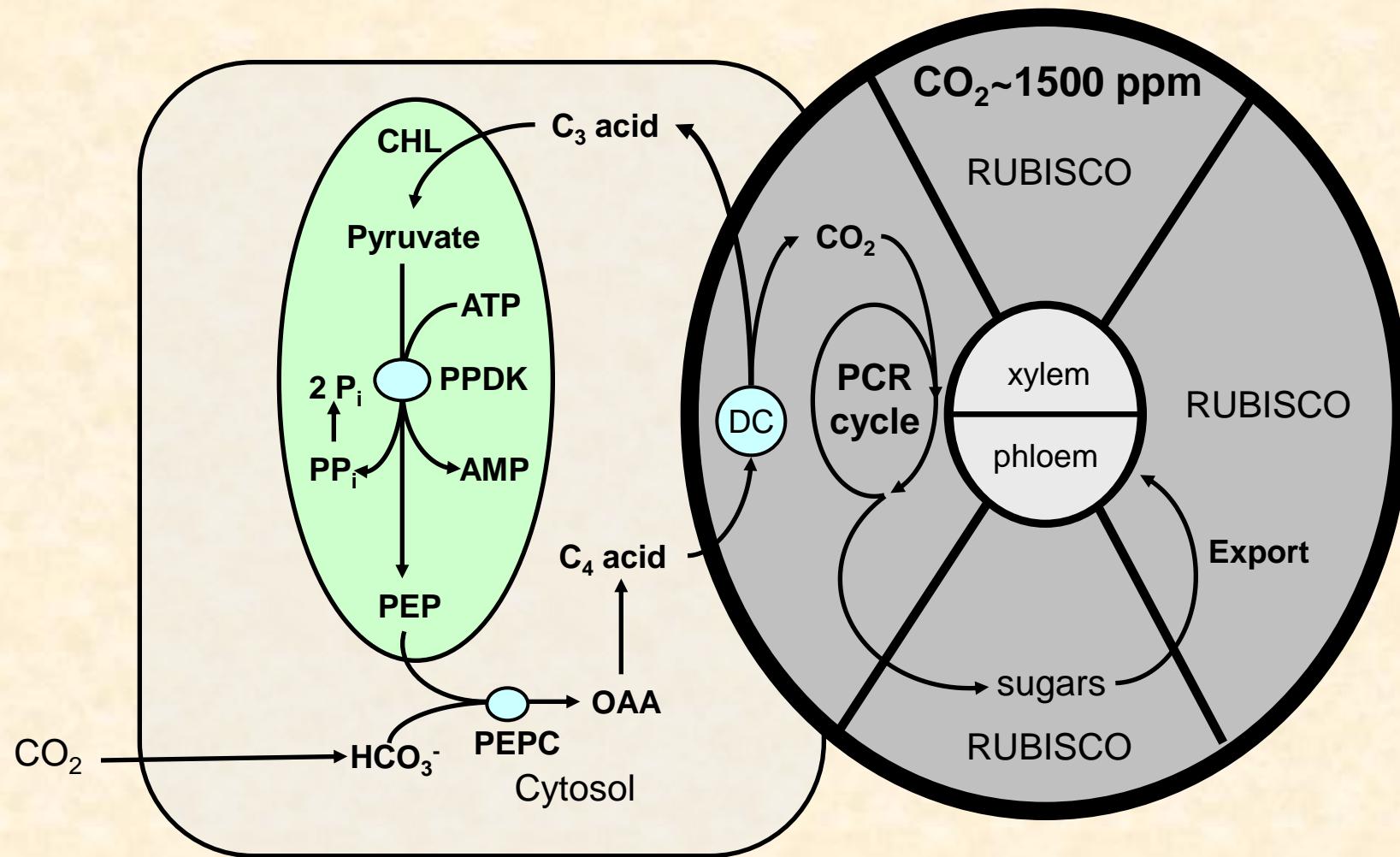


# Theoretical Controls Over C<sub>3</sub> Photosynthesis



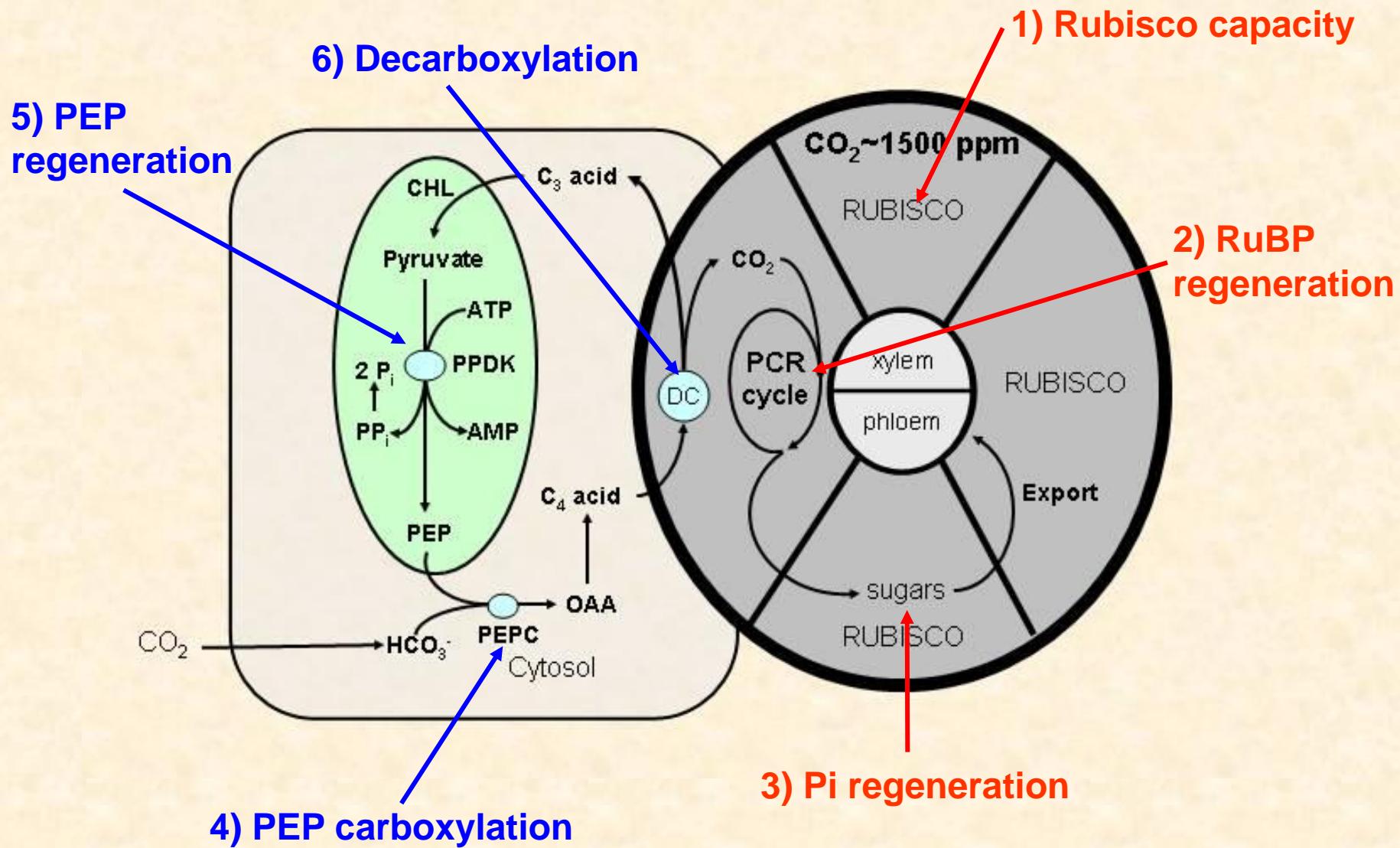
# A Schematic of C<sub>4</sub> Photosynthesis

Mesophyll Tissue      Bundle Sheath Tissue



# Potential Limitations on C<sub>4</sub> Photosynthesis

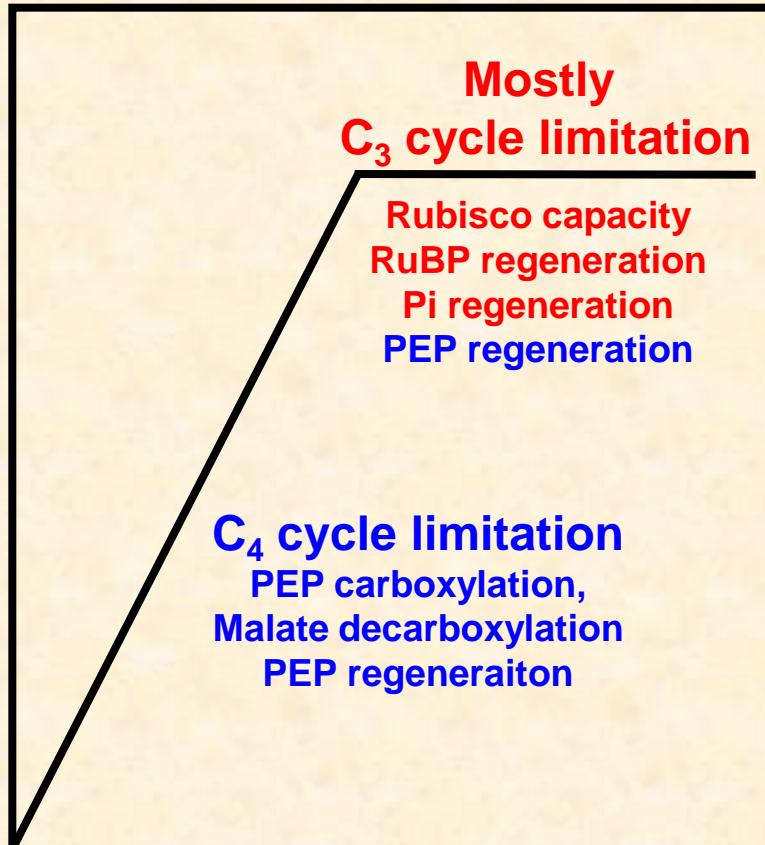
C<sub>4</sub> cycle limitations in blue, C<sub>3</sub> cycle limitations in red



# Limitations of C<sub>4</sub> Photosynthesis

(after von Caemmerer and Furbank (1999) *C<sub>4</sub> Plant Biology*)

Photosynthesis



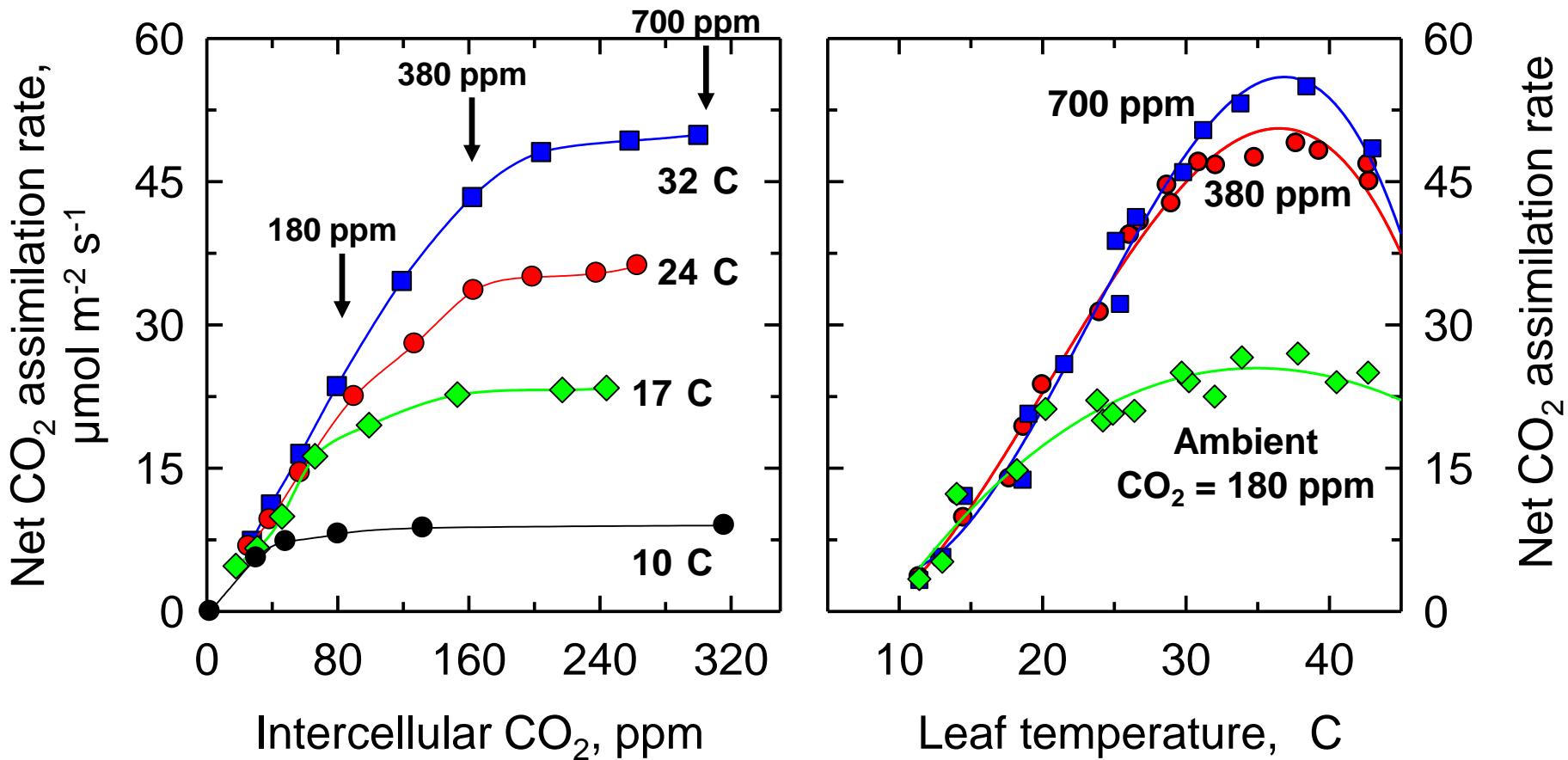
CO<sub>2</sub>

Biochemical models of C<sub>4</sub> photosynthesis predict

- 1) The initial slope of the CO<sub>2</sub> response of photosynthesis generally reflects the strength of the C<sub>4</sub> metabolic pump.
- 2) The CO<sub>2</sub> saturated plateau mainly reflect the strength of the C<sub>3</sub> cycle.

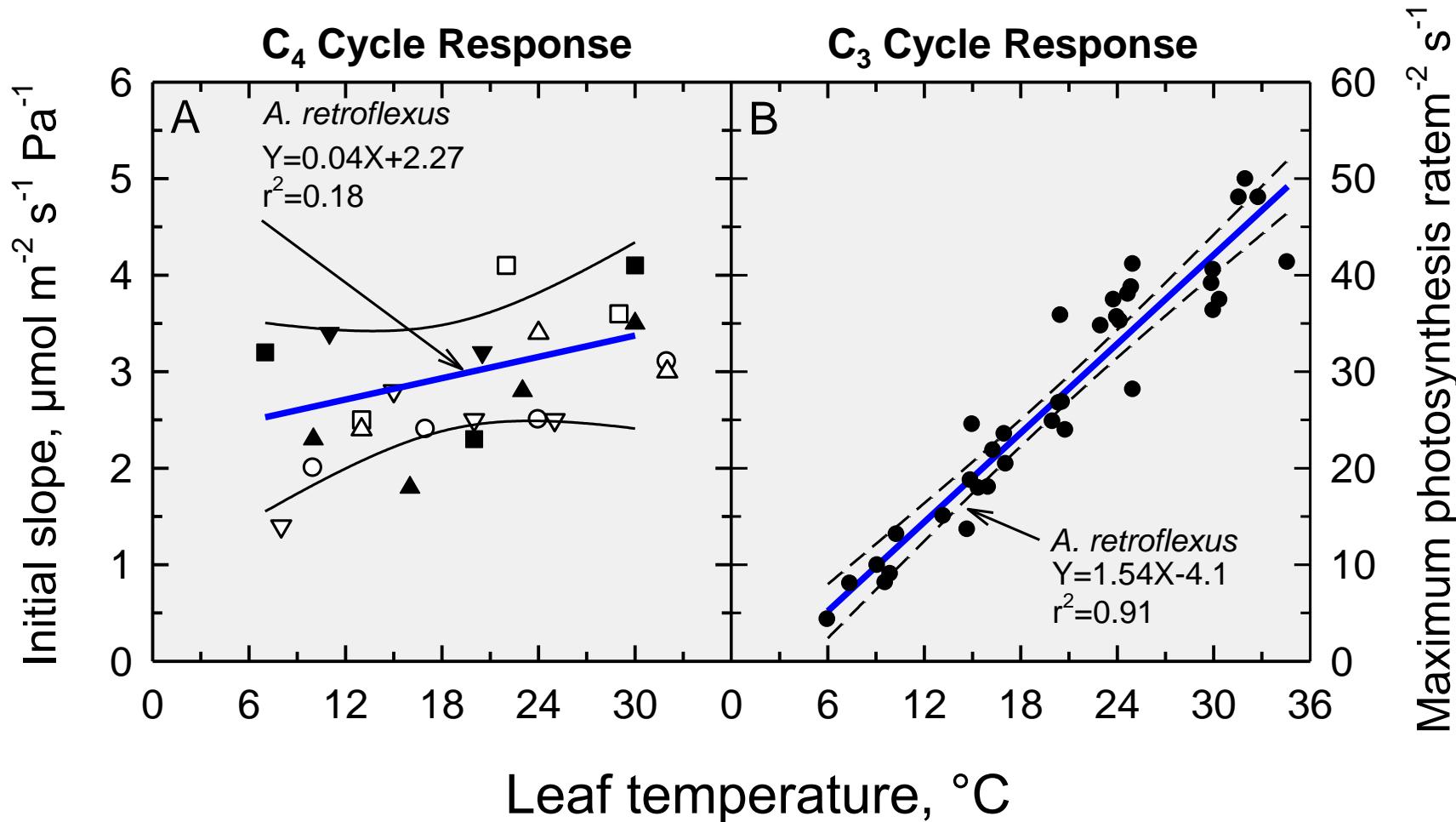
# $C_4$ Photosynthetic Response to $CO_2$ and Temperature

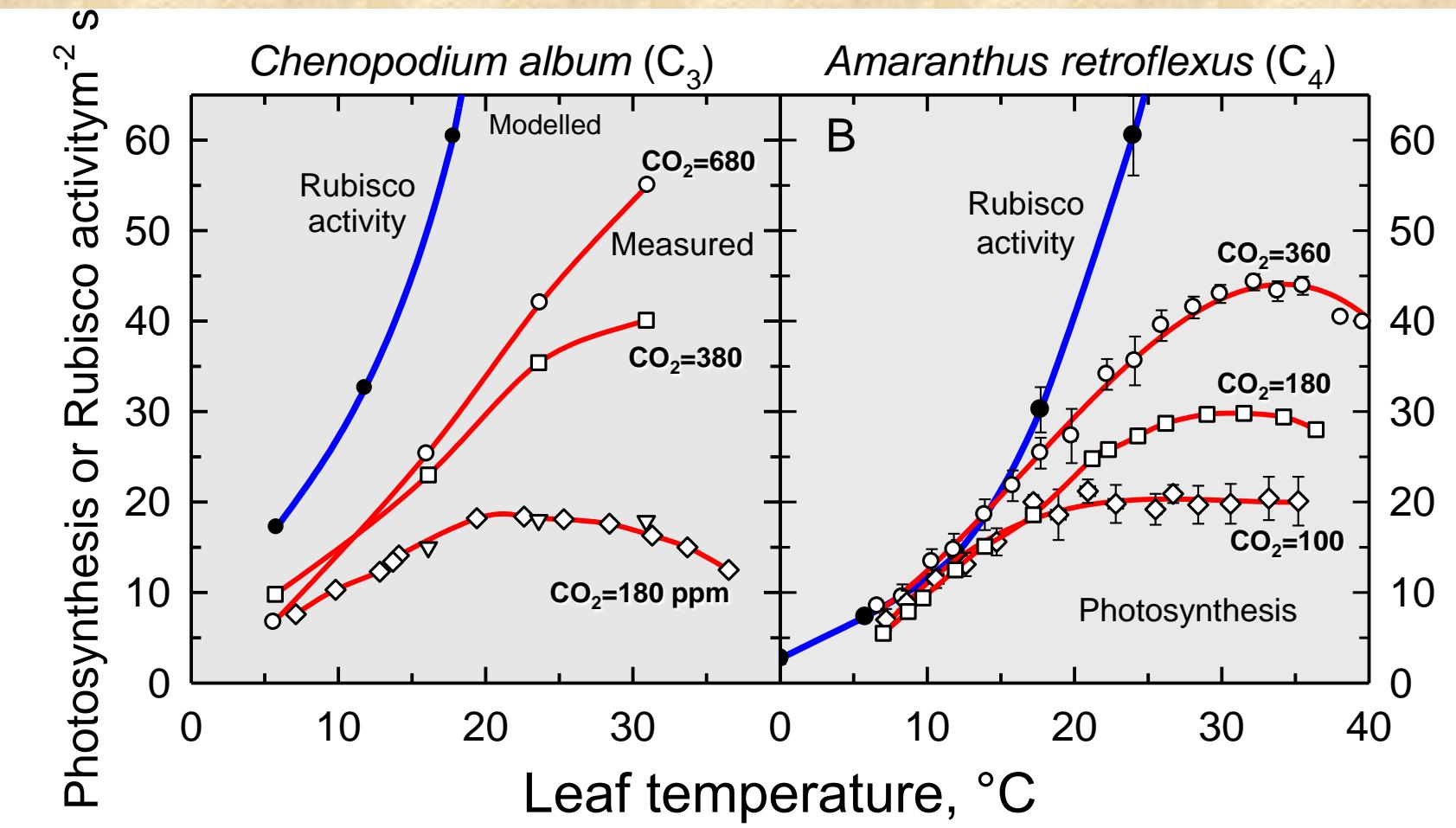
*Amaranthus retroflexus*



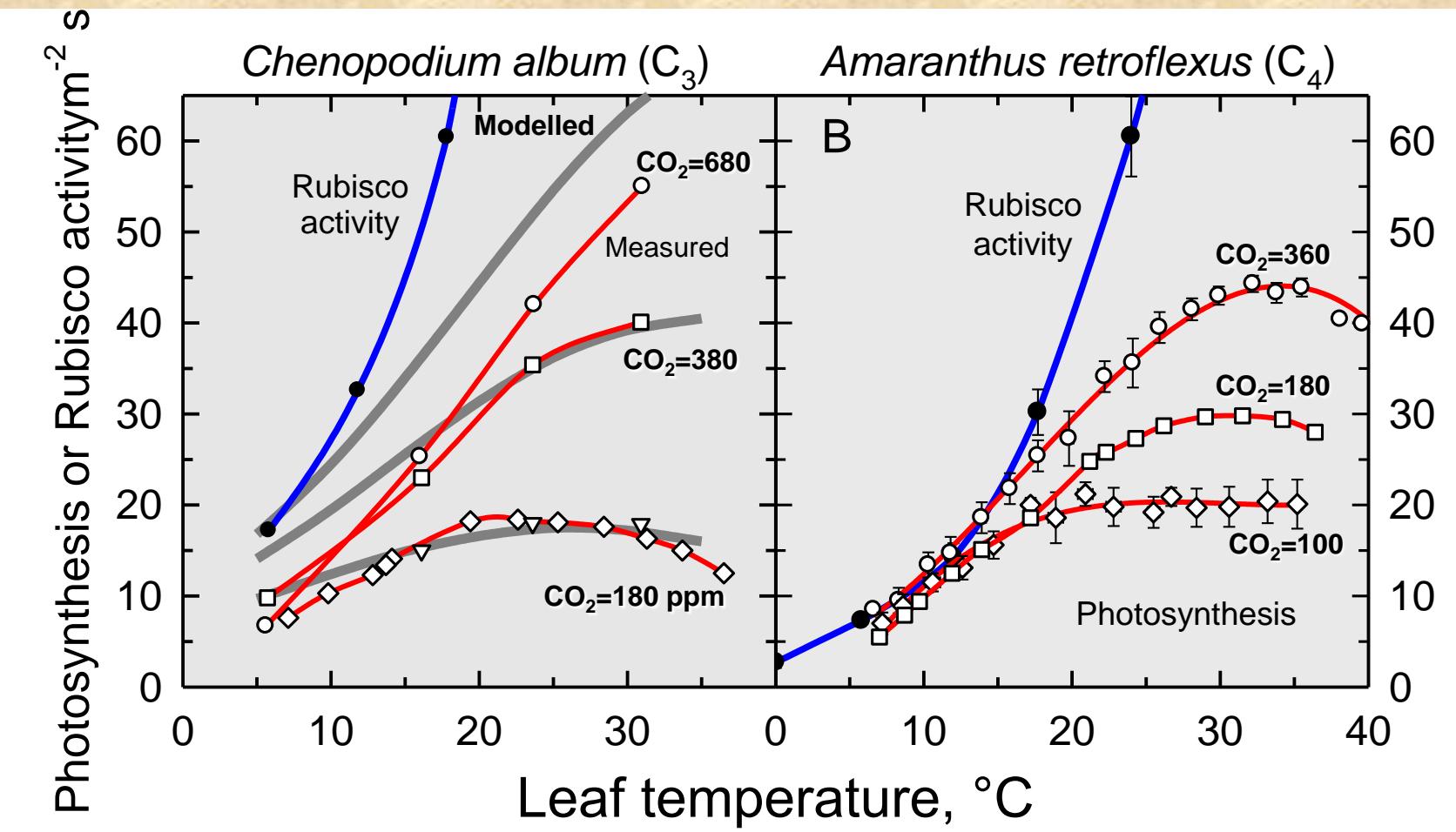
From Sage 2002 J. Exp Bot. 53:609; Sage and Pearcy 2000 Adv. Photosynthesis 9: 497.

# The Effect of Temperature on the Initial Slope and CO<sub>2</sub> Saturated Rate of C<sub>4</sub> Photosynthesis in *Amaranthus retroflexus*



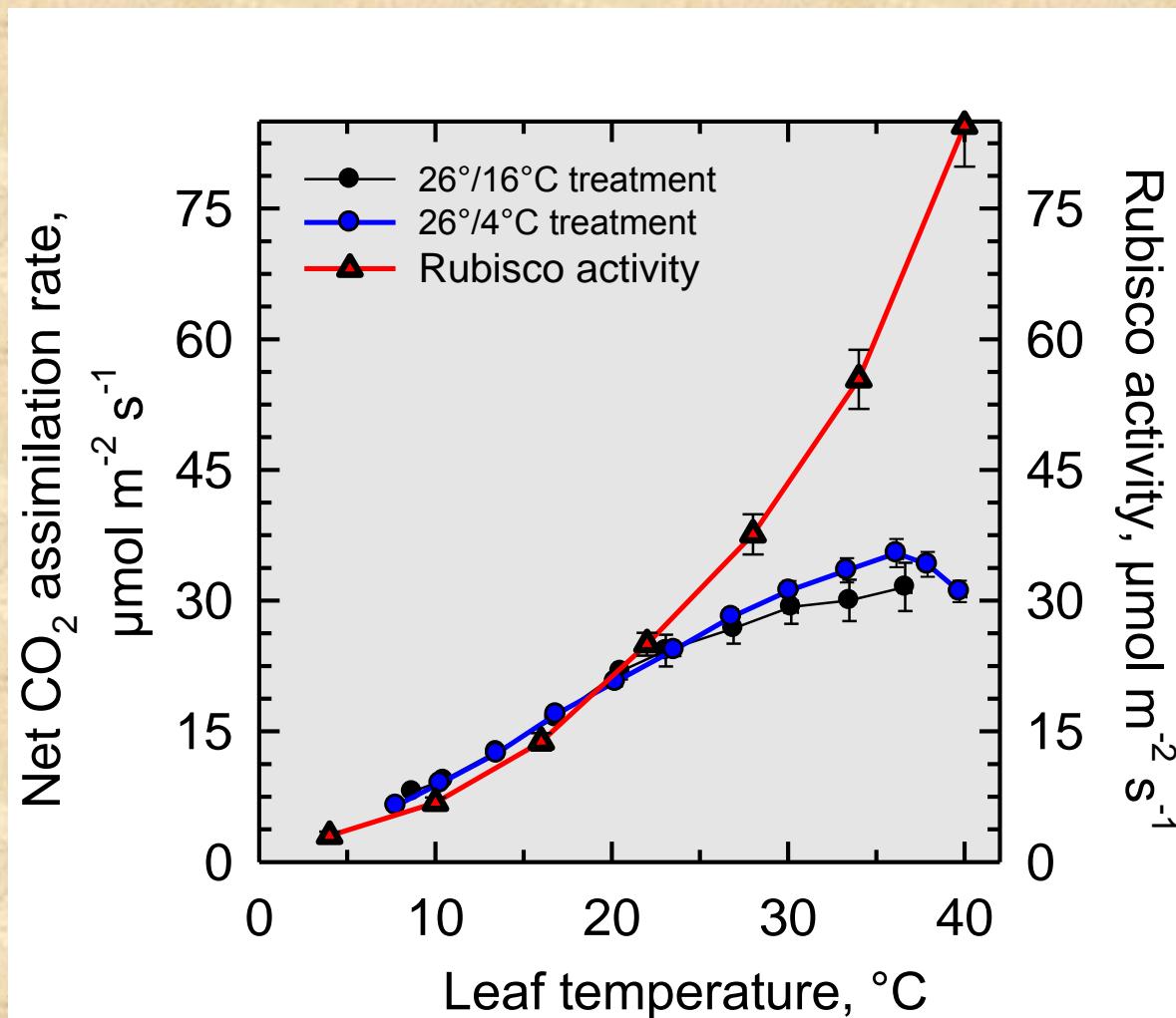


Sage (2002) J. Exp. Bot 53:609 -620



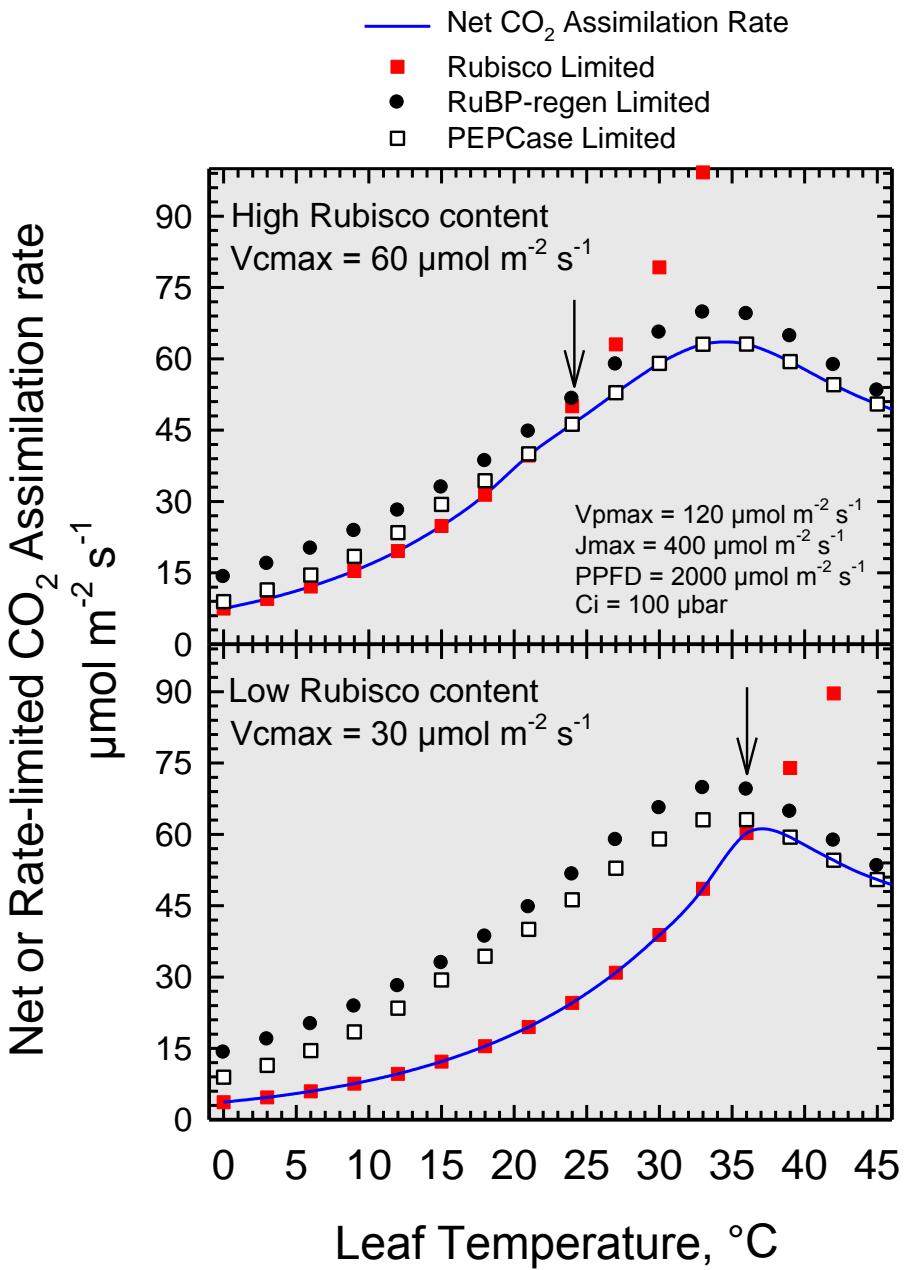
Sage (2002) J. Exp. Bot 53:609 -620

# Photosynthetic Acclimation to Temperature in *Muhlenbergia montanum* A cold adapted C<sub>4</sub> grass from High Elevation



Pittermann and Sage (2001) J. Exp. Bot. 52:829-838

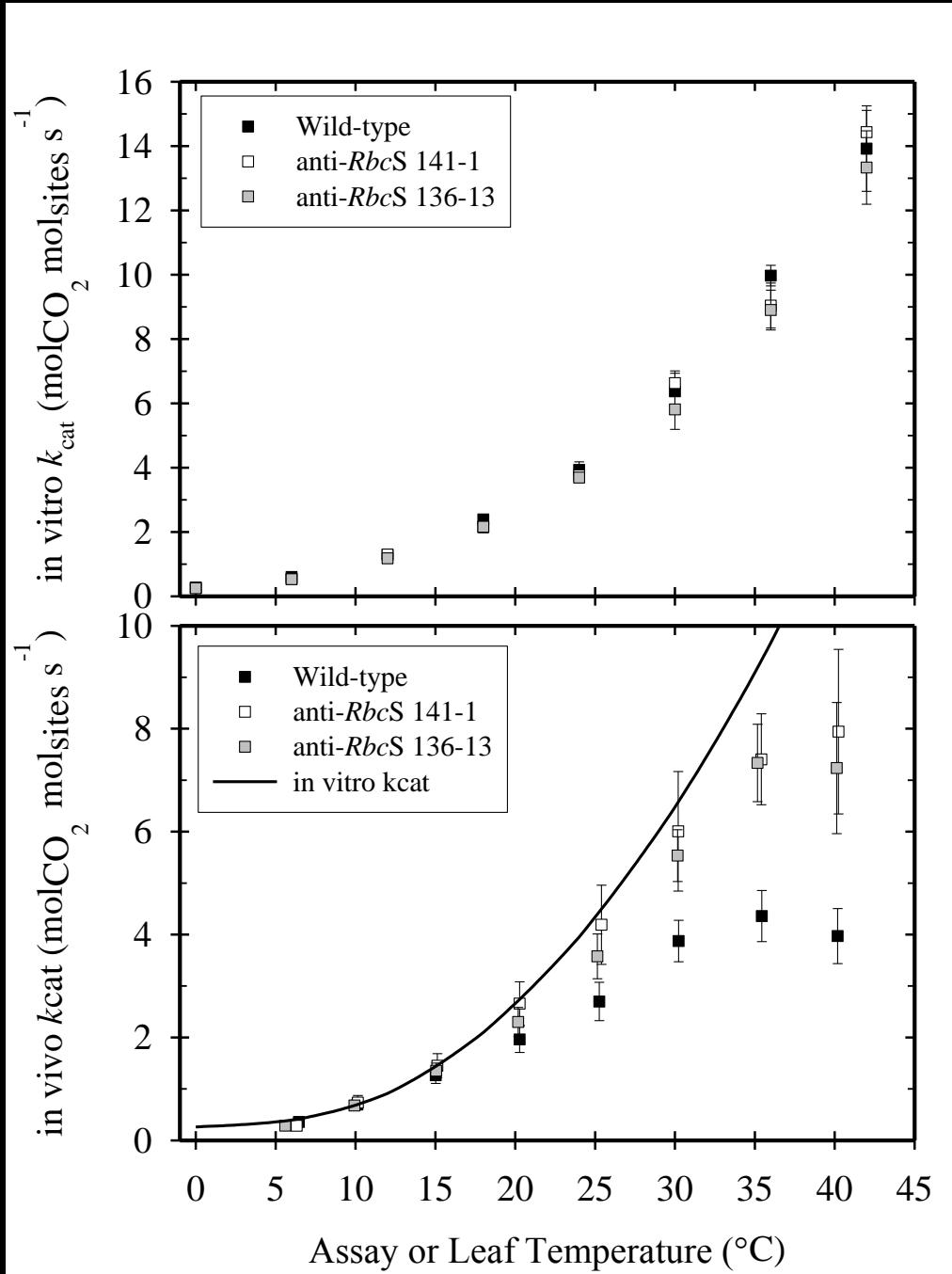
## Modelled Temperature Response of C<sub>4</sub> Photosynthesis



## Measured and Modelled Results from *Flaveria bidentis*



From Kubien, von  
Caemmerer, Furbank and  
Sage (2003) Plant  
Physiology 132: 1577

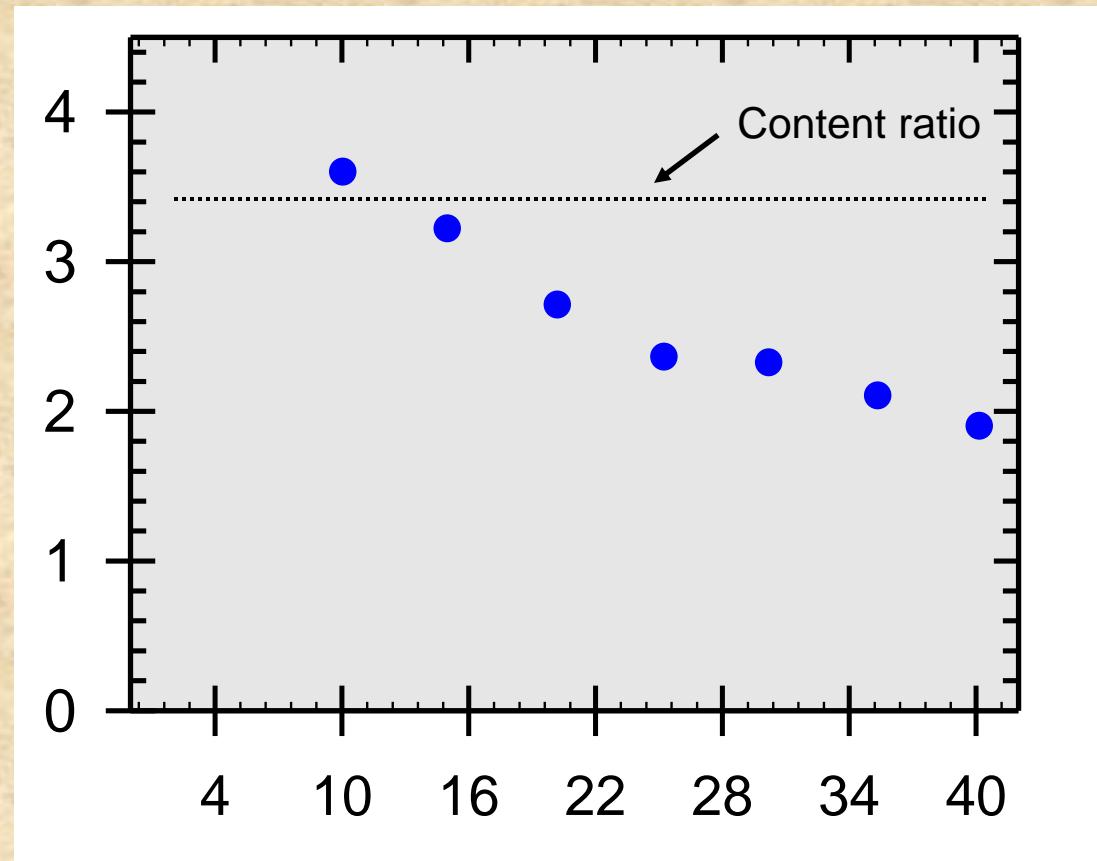


In vitro Rubisco  $K_{\text{cat}}$  equals in vivo Rubisco  $K_{\text{cat}}$  (gross CO<sub>2</sub> assimilation/Rubisco sites) rate in *Flaveria bidentis* at low temperature

From Kubien, von Caemmerer, Furbank and Sage Plant Physiology (in press)

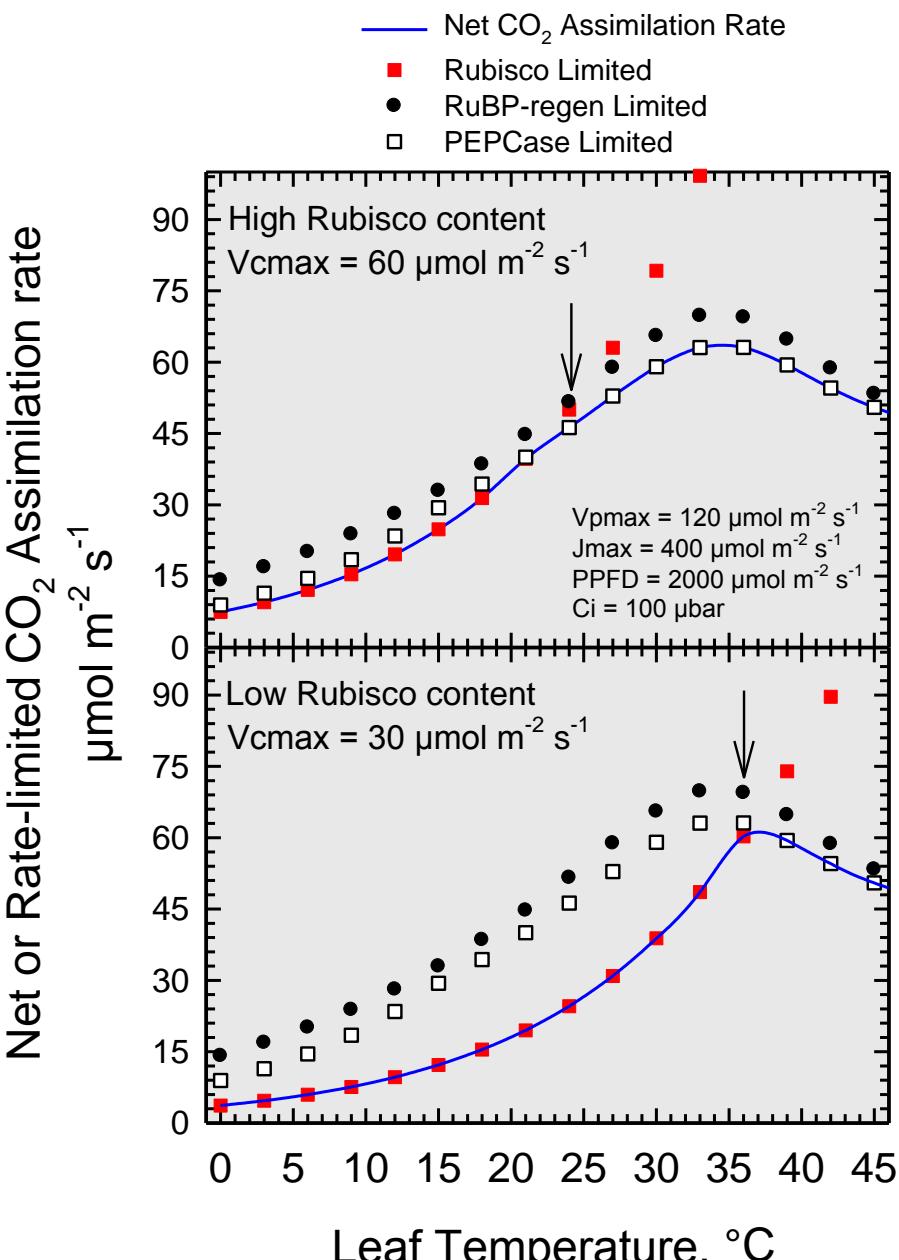
# The Net CO<sub>2</sub> Assimilation Rate of Wild type Relative to Rubisco-Antisense *Flaveria bidentis*

WT / aSSu  
Net CO<sub>2</sub>  
Assimilation  
Rate



Leaf Temperature, °C

## Modelled Temperature Response of C<sub>4</sub> Photosynthesis



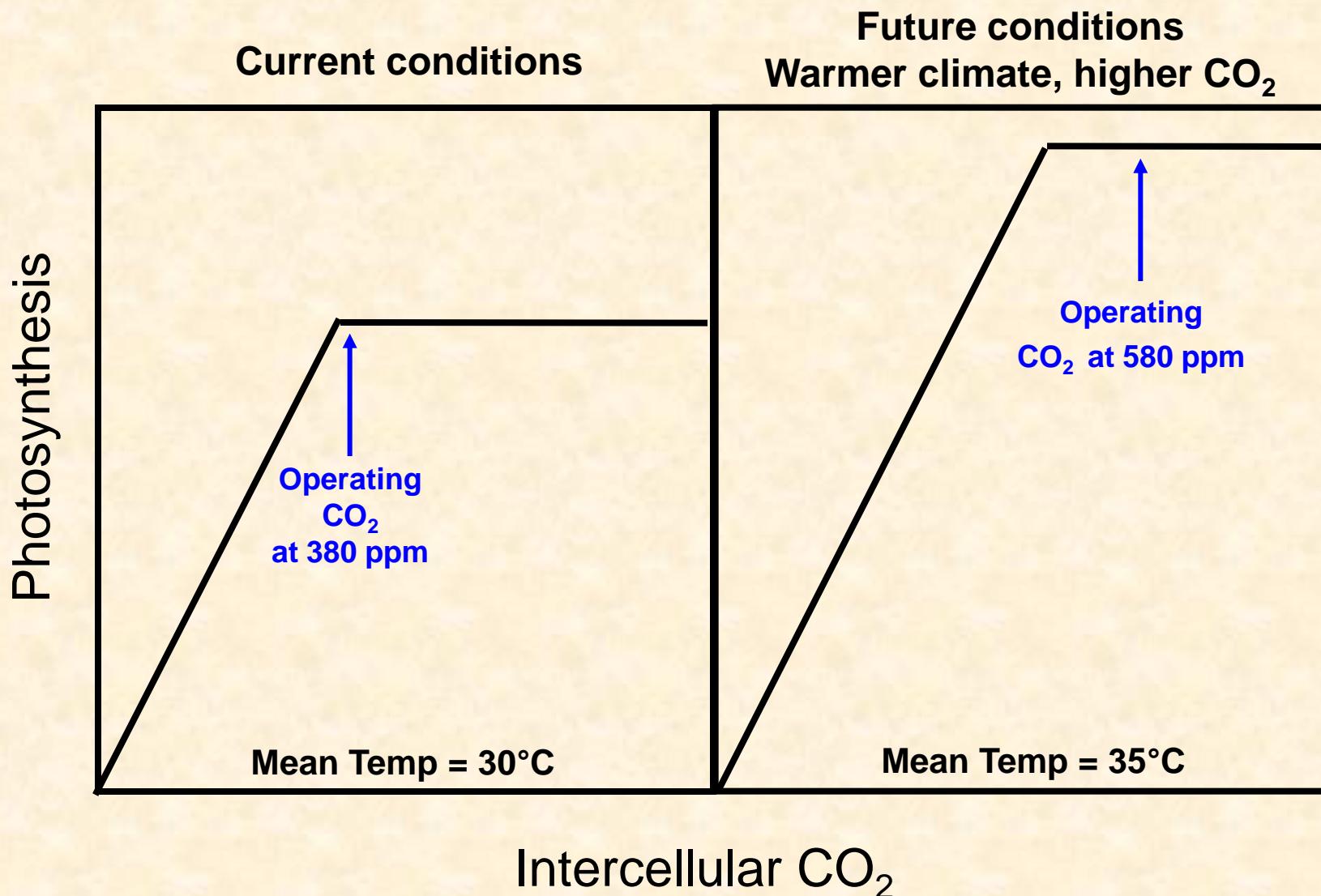
The Limitations on C<sub>4</sub> Photosynthesis Above the Thermal Optimum Are Not Clear.

### Leading Proposals:

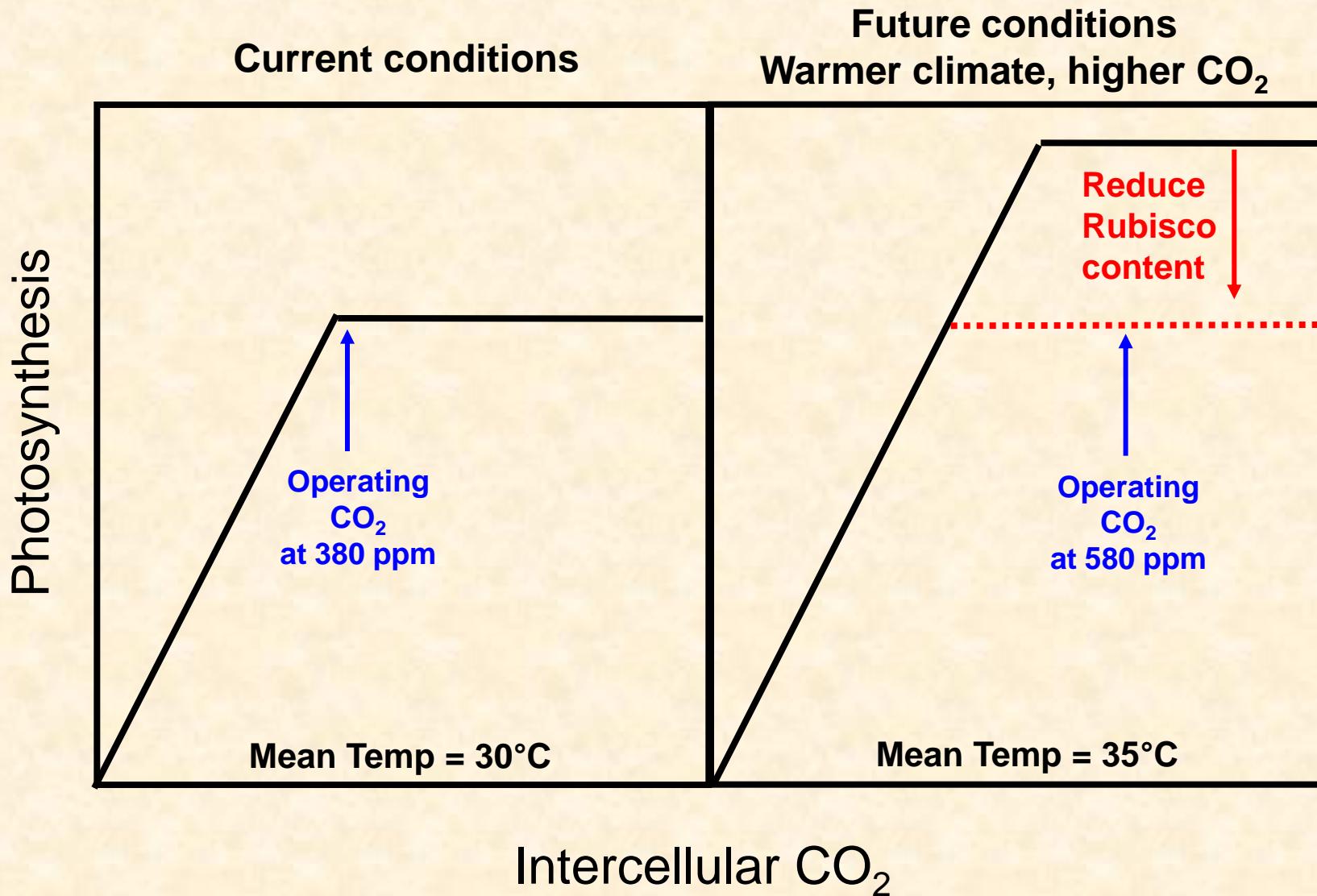
- 1) PEP carboxylation Capacity
- 2) Electron Transport
- 3) Rubisco activation state
- 4) PEP regeneration

It is not the capacity of Rubisco to consume RuBP.

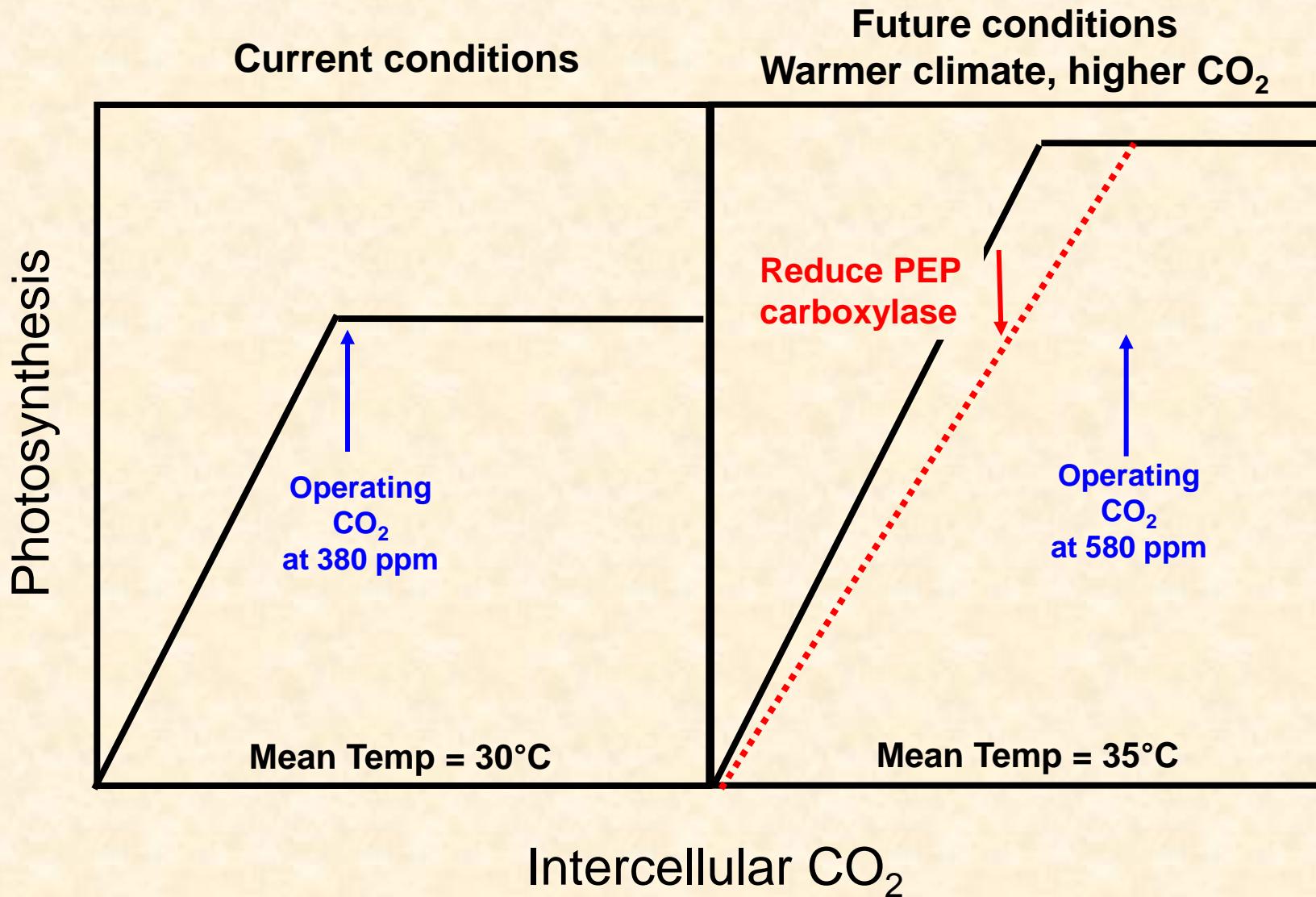
# C<sub>4</sub> Photosynthesis Provides Many Options for Responding to Global Climate Change



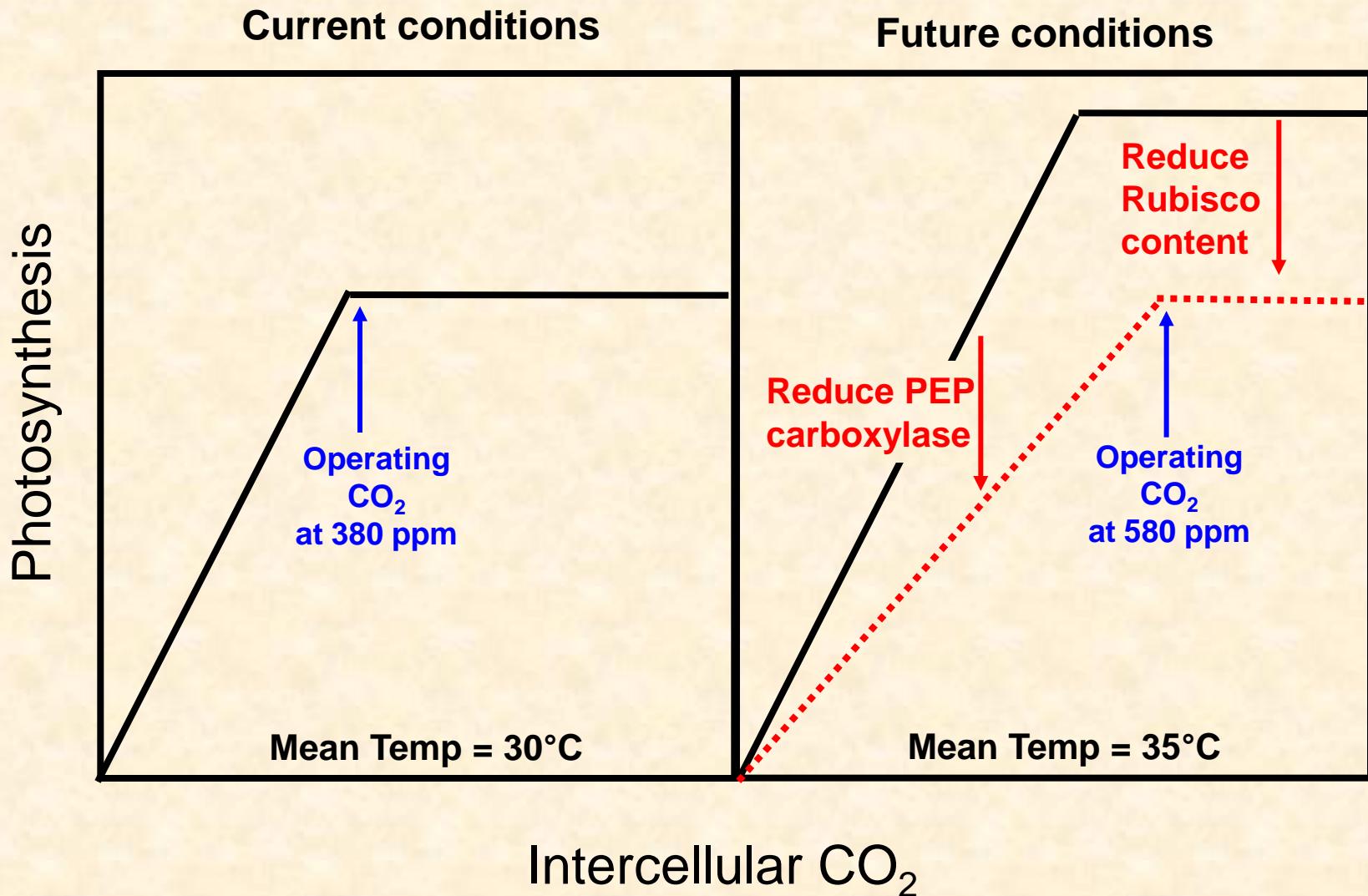
# Scenario 1: Improve Nitrogen Use Efficiency by Reducing Rubisco Investment



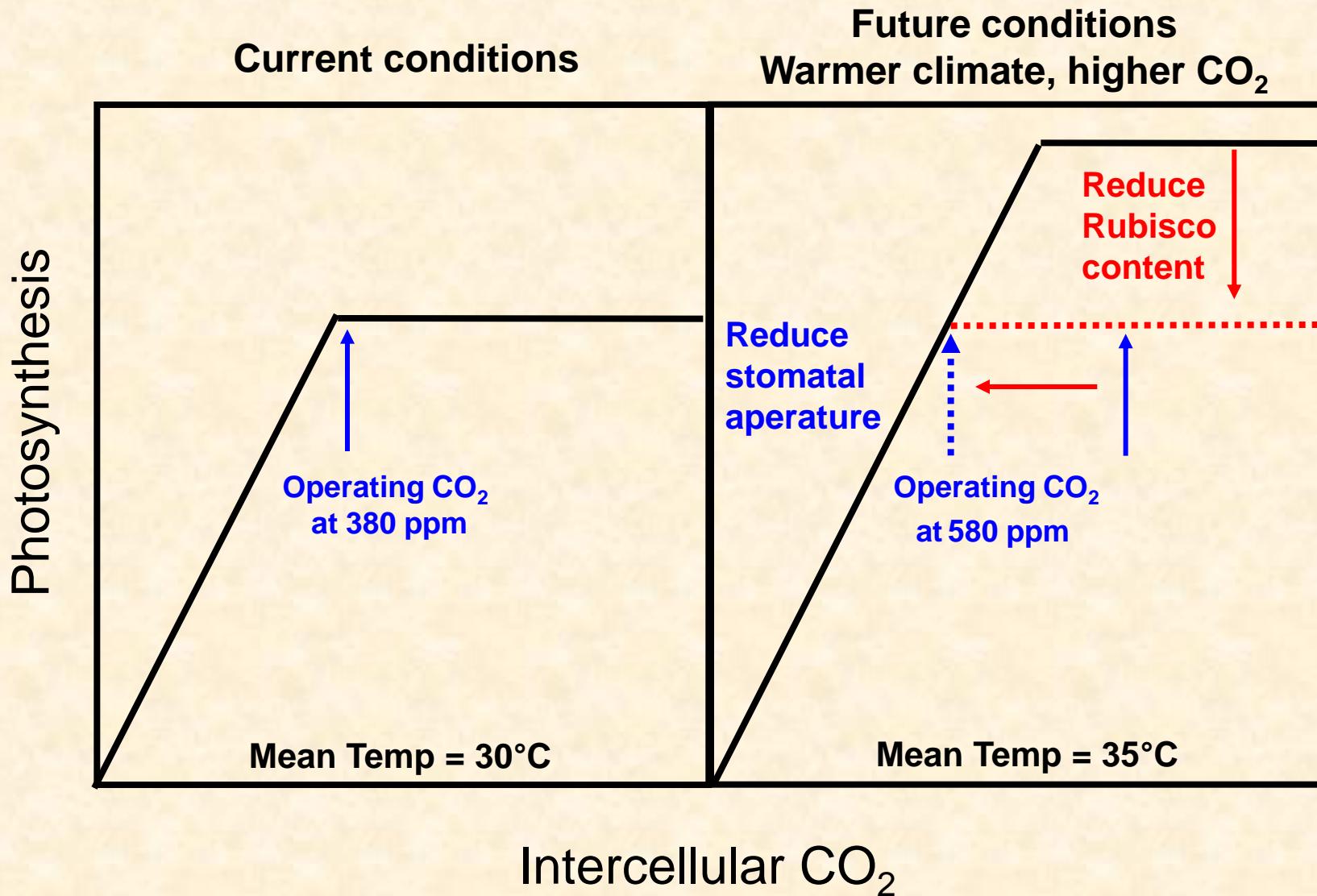
## Scenario 2: Improve Nitrogen Use Efficiency by Reducing PEP Carboxylase Investment

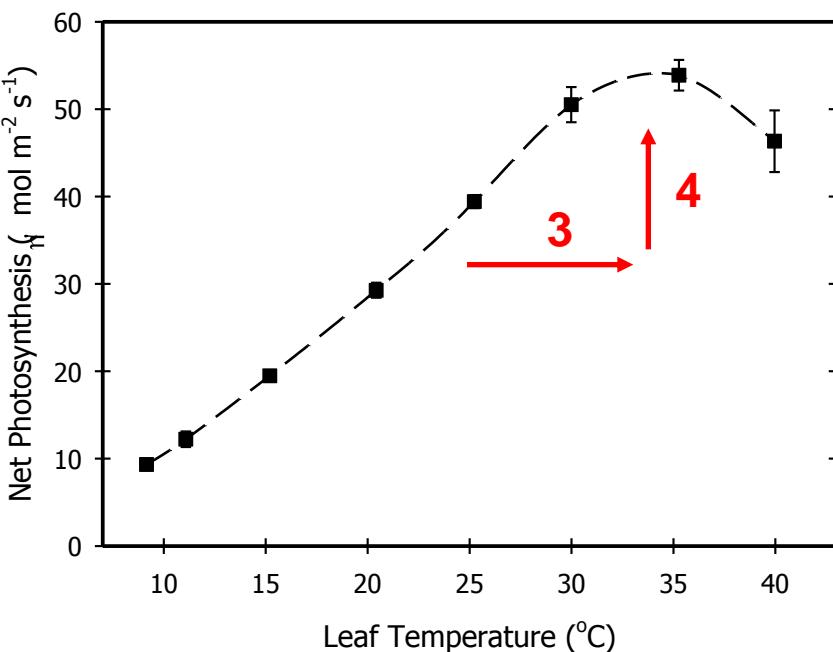
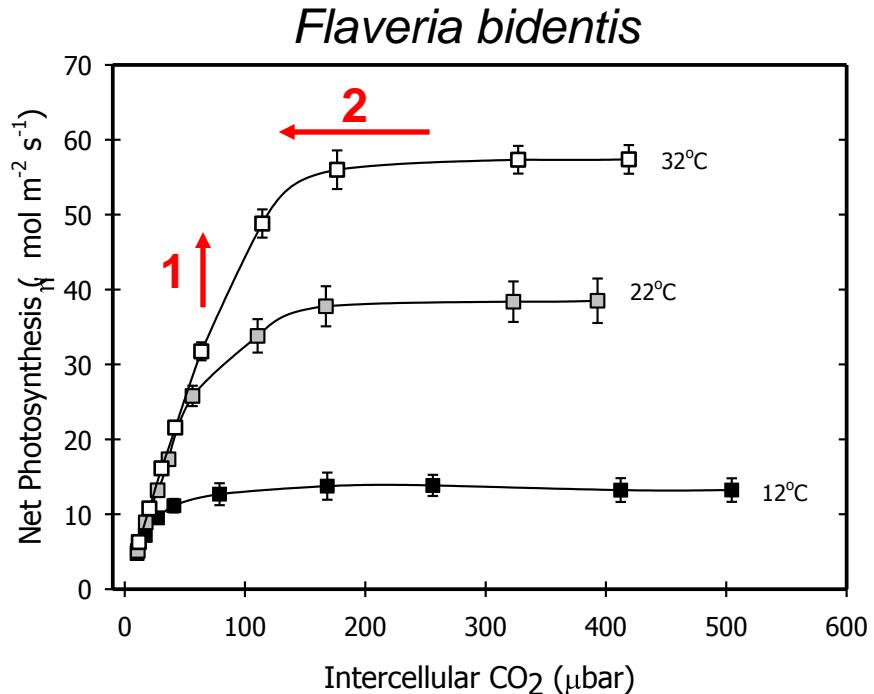


# Scenario 3: Improve Nitrogen Use Efficiency by Reducing Both Carboxylases



## Scenario 4: Improve Nitrogen Use Efficiency and Water Use Efficiency

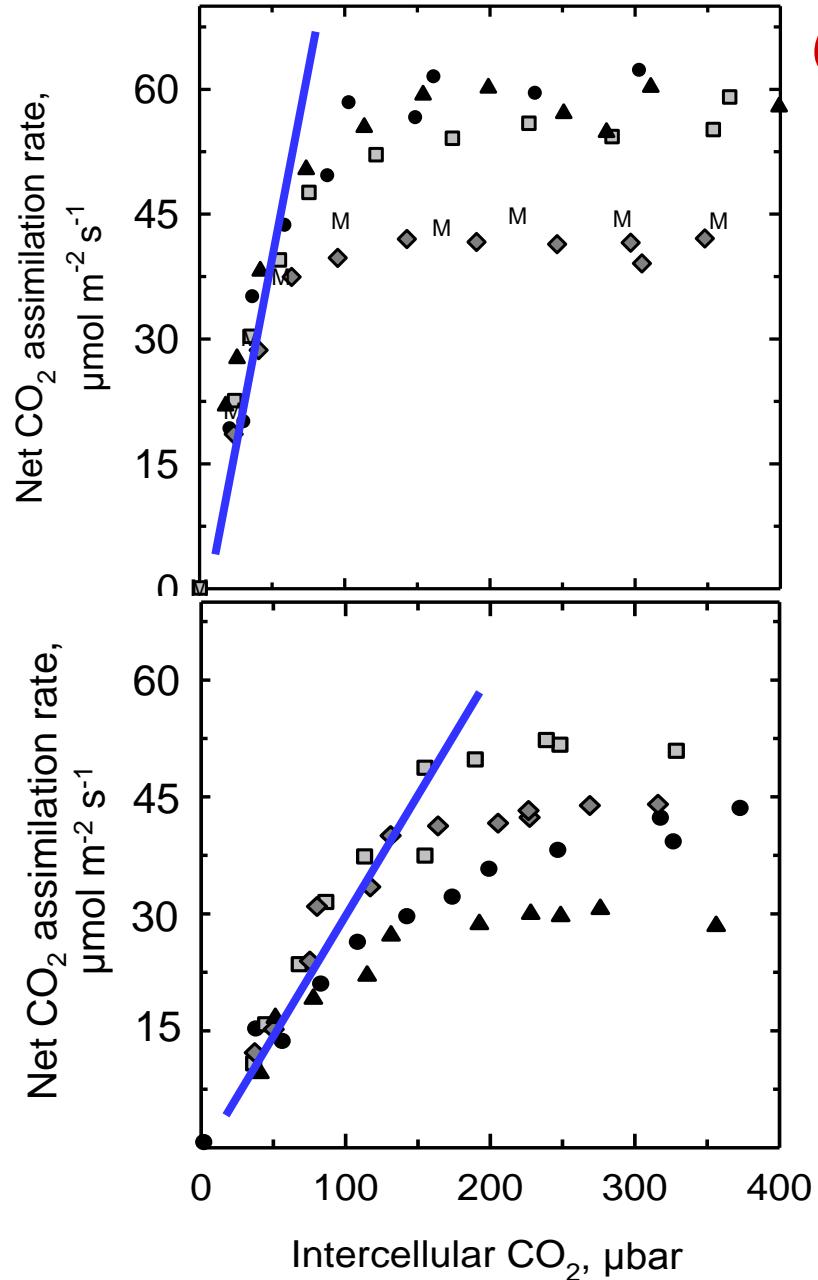




## Scenario 5: Improve WUE and Photosynthesis

1. Increase the strength of the C<sub>4</sub> pump
2. Selectively reduce stomatal conductance and the operational CO<sub>2</sub>
3. Lower transpiration saves water and increases canopy temperature
4. A warm canopy stimulates C<sub>4</sub> gas exchange
5. High photosynthesis maximizes light use efficiency

# Gas Exchange Responses



*Calligonum caput-medusae*

Carboxylation efficiency (CE) 0.78  
 $\mu\text{mol m}^{-2} \text{s}^{-1} \mu\text{bar}^{-1}$



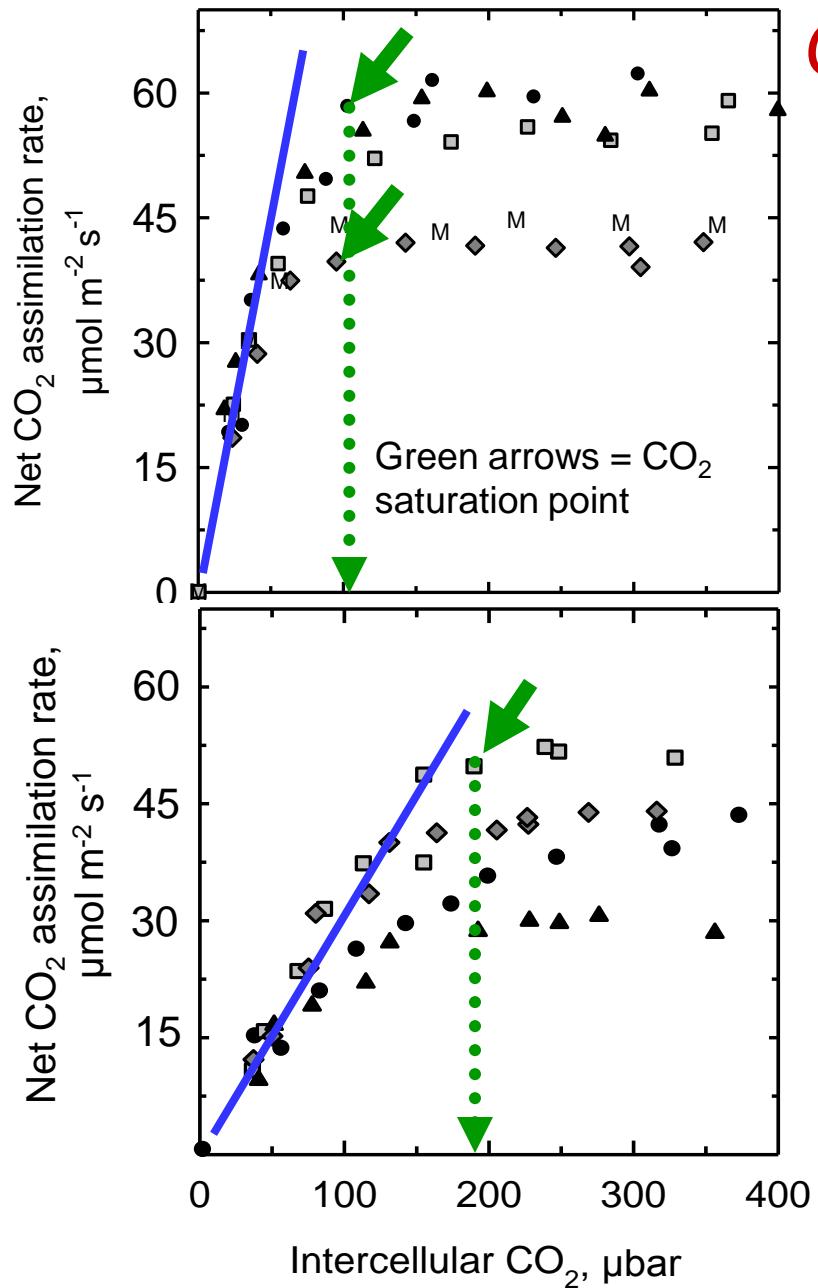
\* Each symbol  
represents a separate  
individual, **M** = *C.  
microcarpum*

*Haloxylon aphyllum*

Carboxylation efficiency (CE) 0.31  
 $\mu\text{mol m}^{-2} \text{s}^{-1} \mu\text{bar}^{-1}$



# RESULTS: A. Gas-exchange:



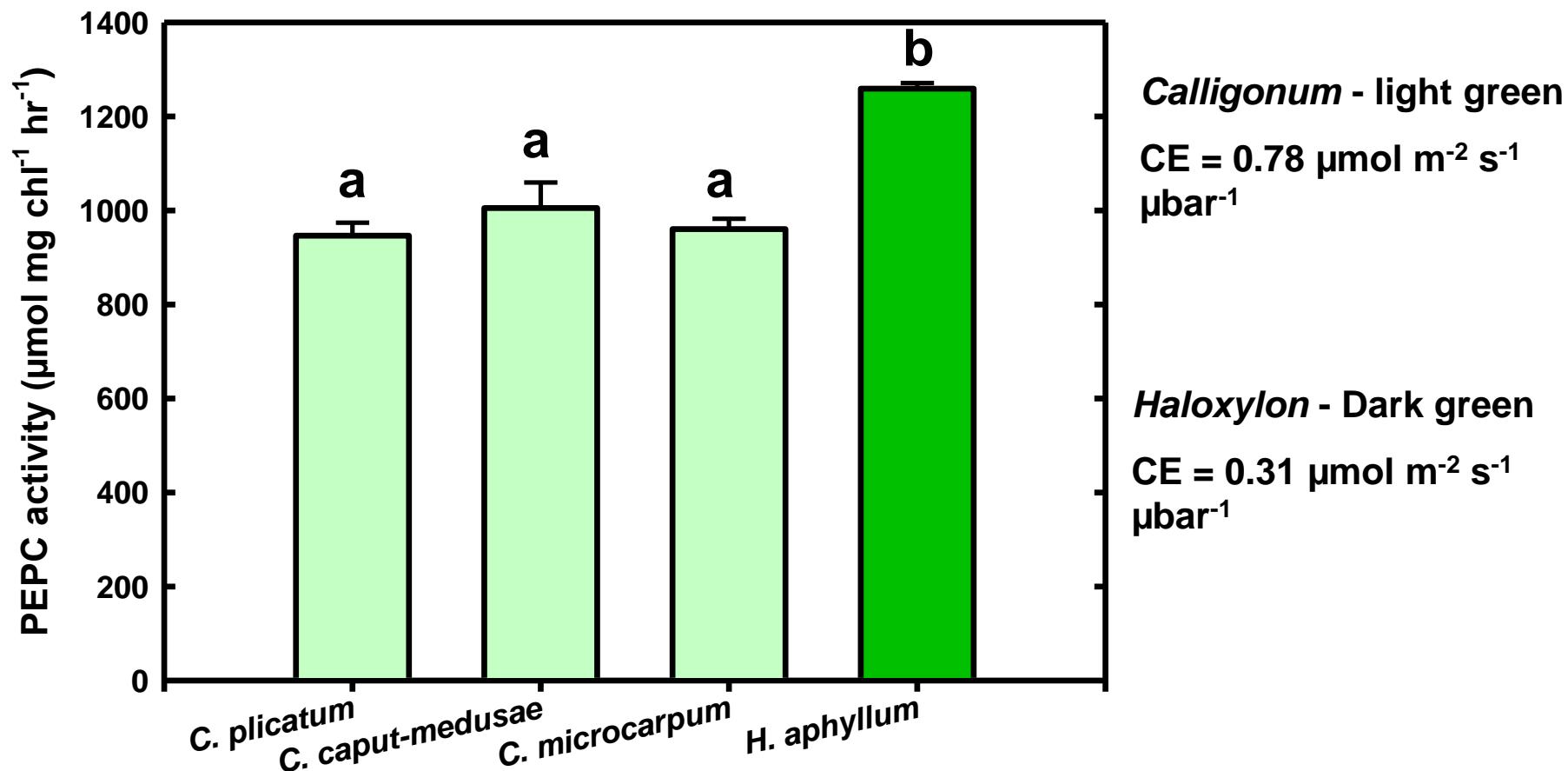
*Calligonum caput-medusae*

*Calligonum* is more effective than *Haloxylon* in concentrating  $\text{CO}_2$  around Rubisco at limiting  $\text{CO}_2$  levels

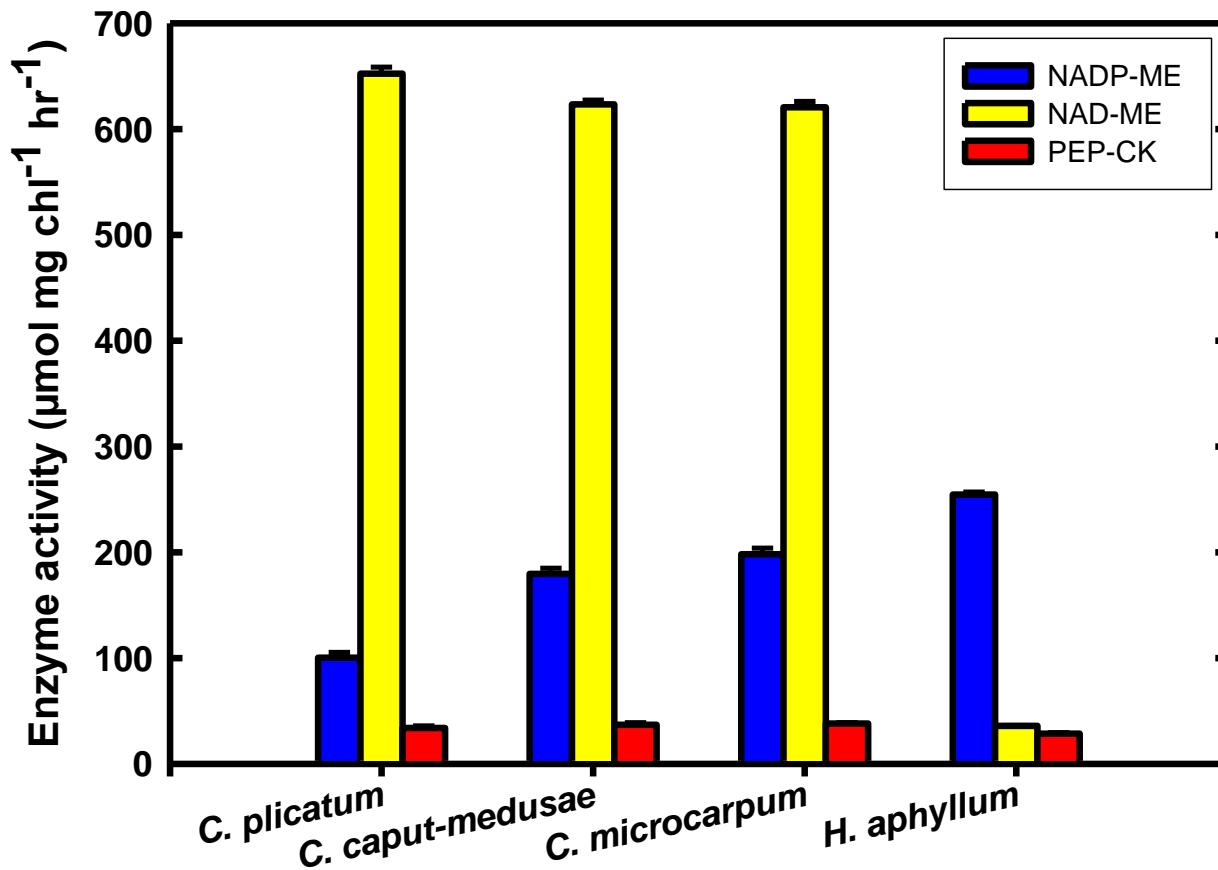
What might contribute to these differences?

*Haloxylon aphyllum*

# PEP Carboxylase activity



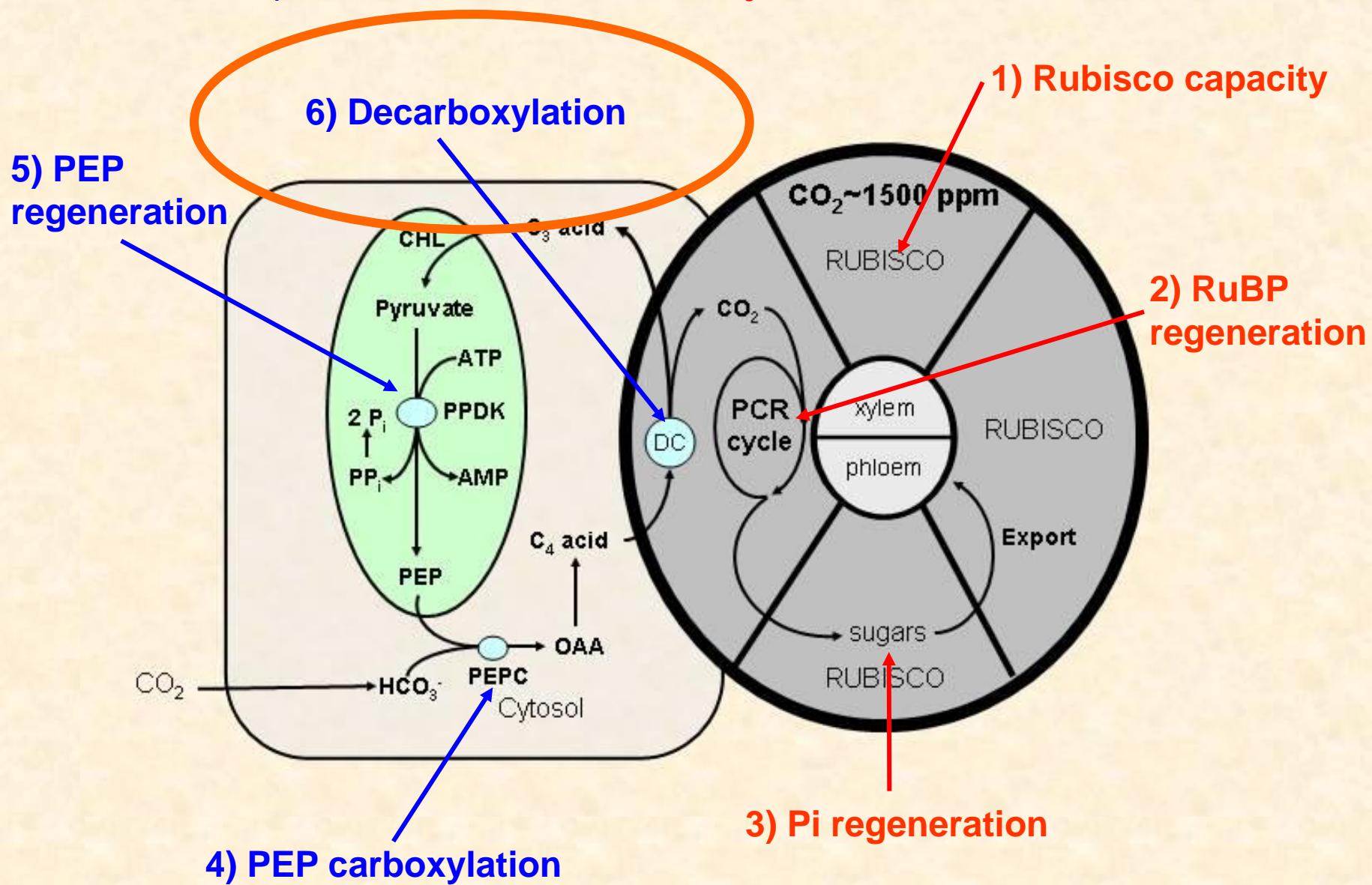
# Activities of Decarboxylating Enzymes



(Muhaidat, Dengler and Sage, In prep)

# Potential Limitations on C<sub>4</sub> Photosynthesis

C<sub>4</sub> cycle limitations in blue, C<sub>3</sub> cycle limitations in red



# Summary

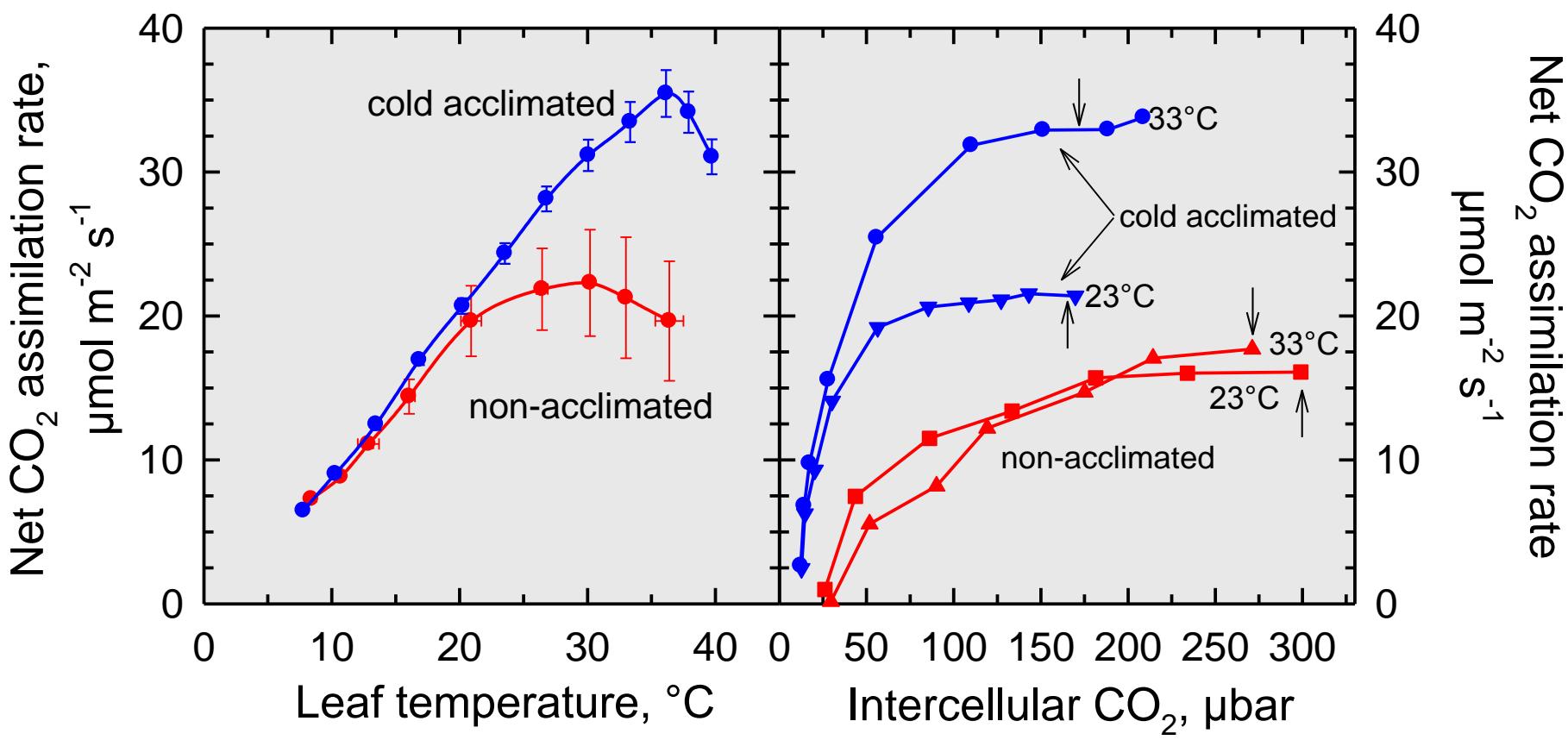
- C<sub>4</sub> photosynthesis is limited by Rubisco capacity at cooler temperatures, although short-term cold exposure can also impair PPDK.
- The limitation on C<sub>4</sub> photosynthesis at elevated temperature remains unclear.
- In a warmer, high CO<sub>2</sub> world, it is possible to improve WUE and NUE without impairing photosynthesis by manipulating enzyme contents in the C<sub>3</sub> and C<sub>4</sub> cycles of a C<sub>4</sub> crop such as sugar cane.

Many Thanks to David Kubien (on the left), my PhD student who worked on *Flavaria bidentis*



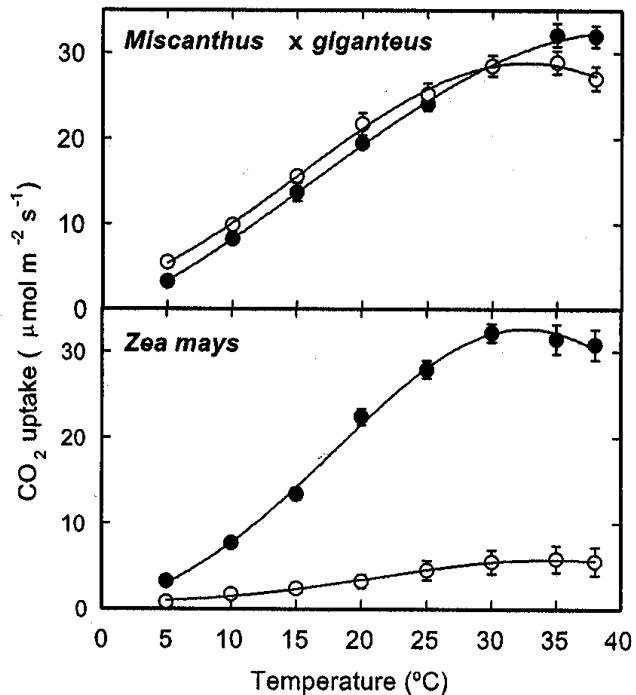
# Photosynthetic Response following Transfer to Night Cold ( $4^{\circ}\text{C}$ )

*Muhlenbergia montanum*

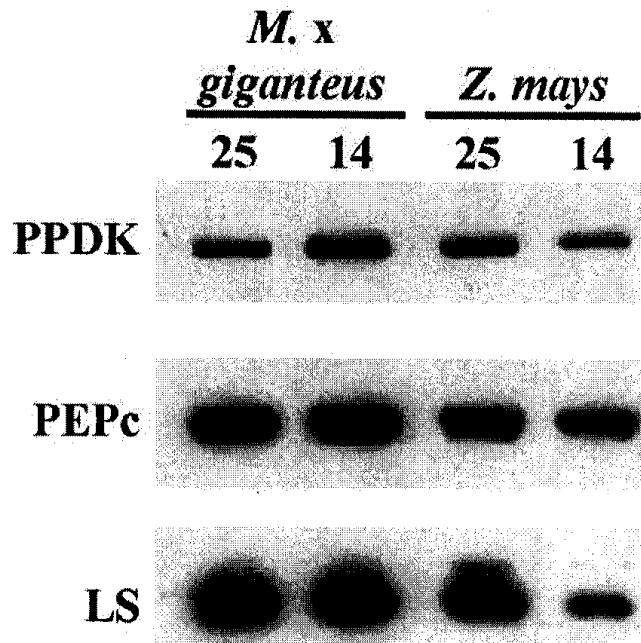


Pittermann and Sage (2001) J. Exp. Bot. 52:829-838

# Cold-acclimation in *Miscanthus x giganteus* and cold-stress in *Zea mays*



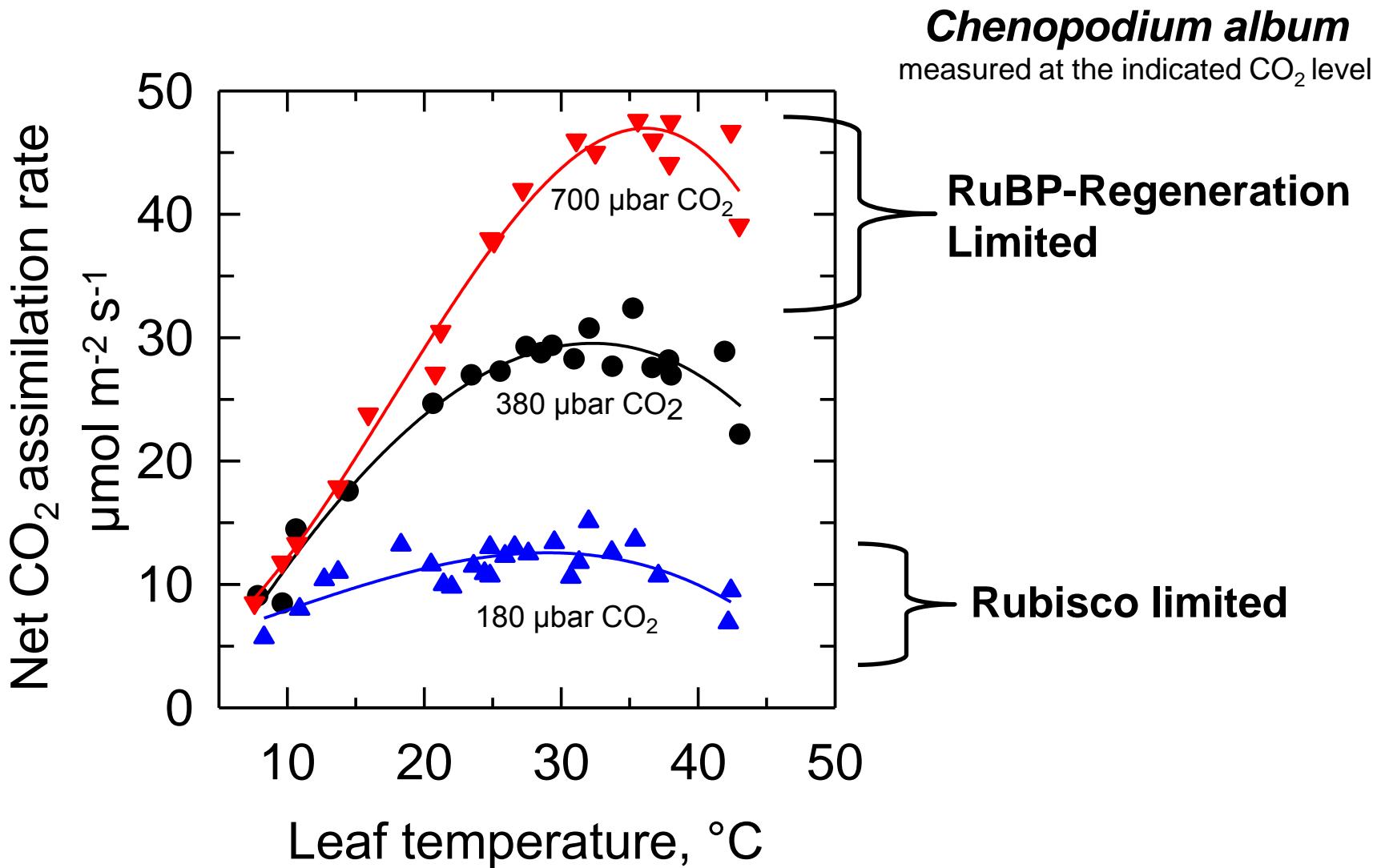
**Figure 1.** Temperature response of photosynthetic  $\text{CO}_2$  uptake per unit leaf area for *M. x giganteus* and maize grown at 25°C/20°C or 14°C/11°C day/night temperatures. Error bars ( $\pm 1 \text{ SE}$ ) of the mean ( $n = 8-15$ ) are shown, except when smaller than the symbol size.

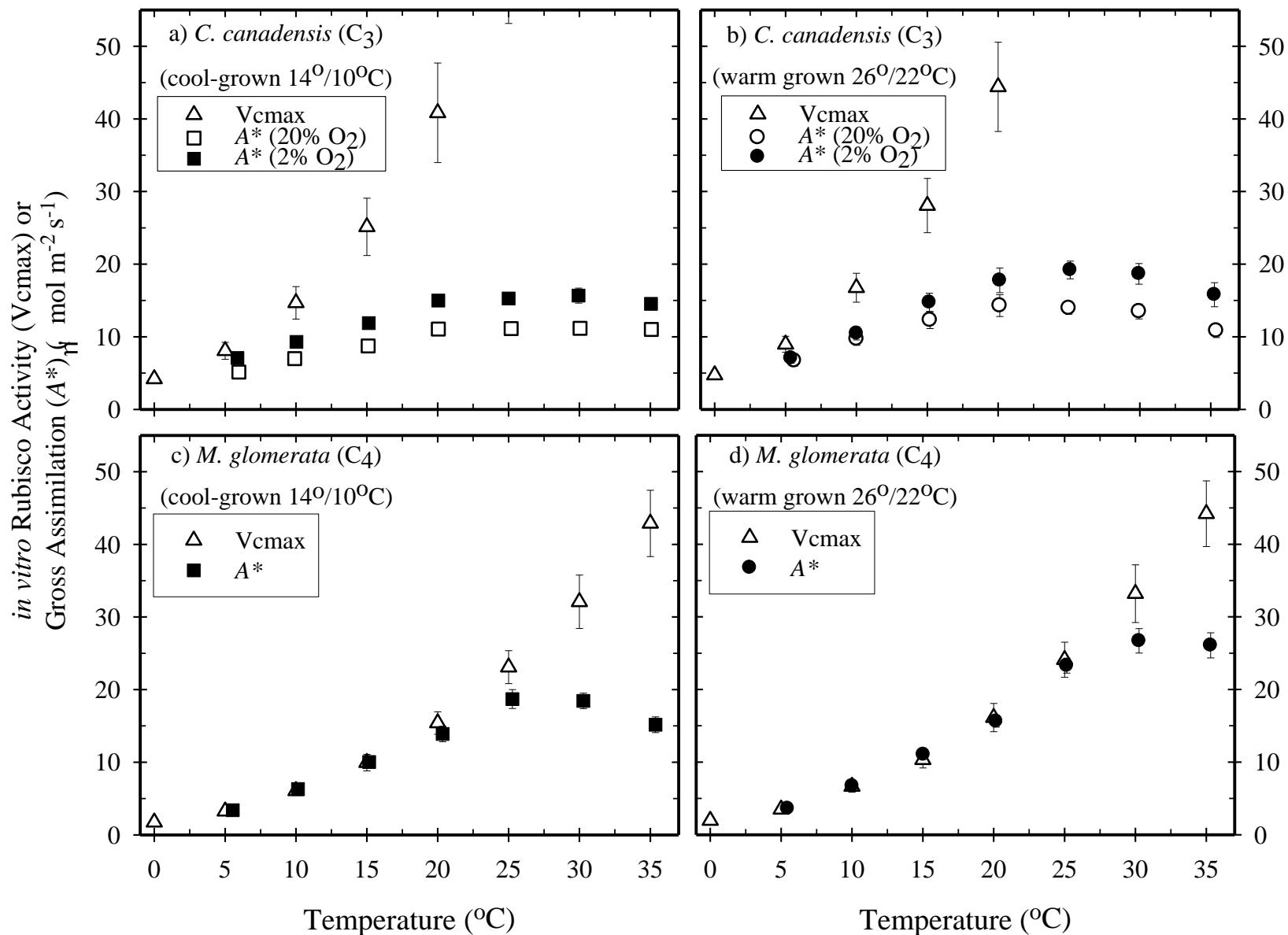


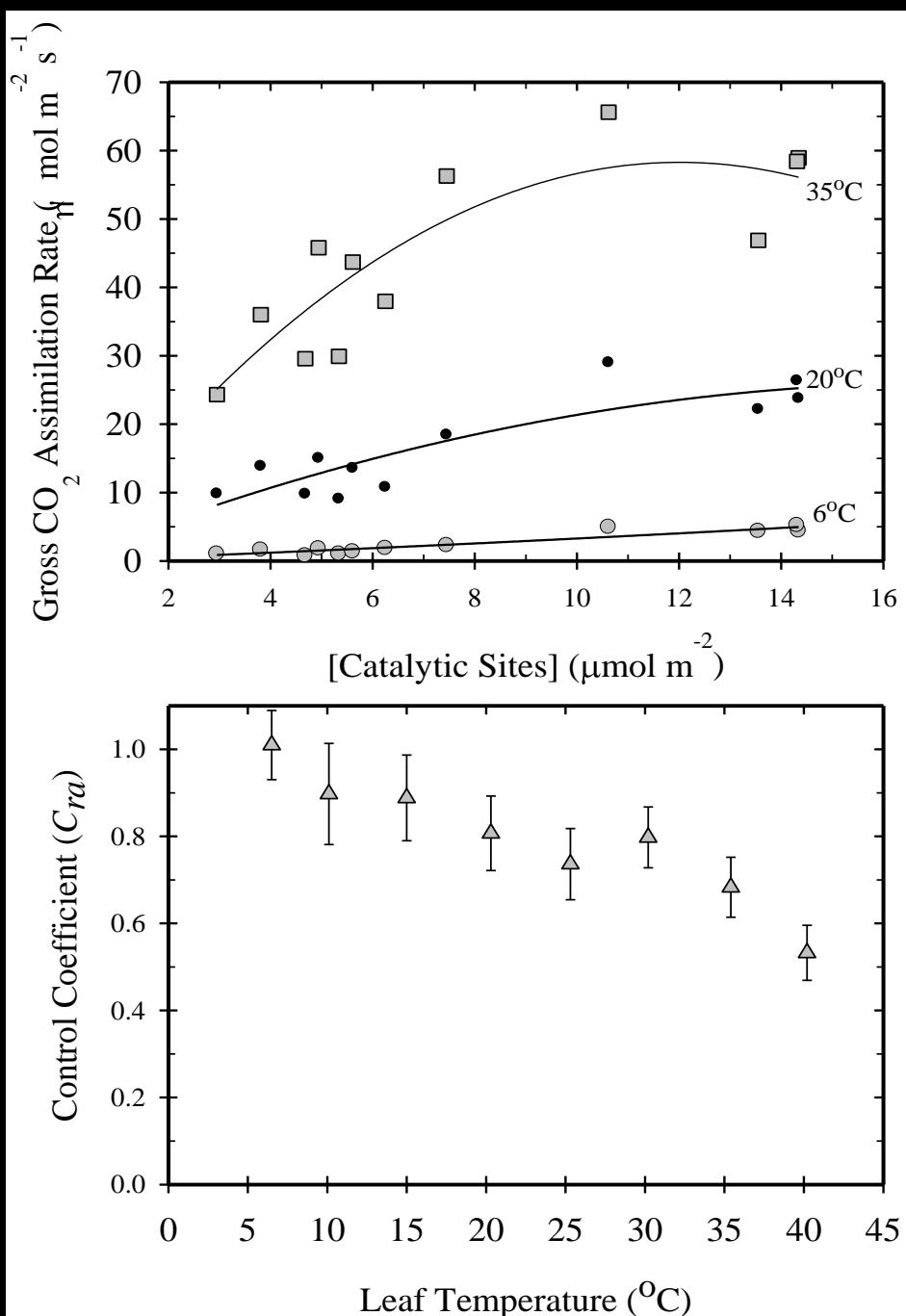
**Figure 2.** Sample western blot of PPDK, PEPC, and the large subunit of Rubisco (LS) extracted from *M. x giganteus* and maize leaves grown at 25°C/20°C or 14°C/11°C day/night temperatures. Samples were loaded on an equal leaf area basis.

Naidu, Moose, Al-Shoaibi et al. (2003) Plant Physiol. 132:1688

# Possible Limitations on C<sub>3</sub> Photosynthesis at High and Low CO<sub>2</sub>



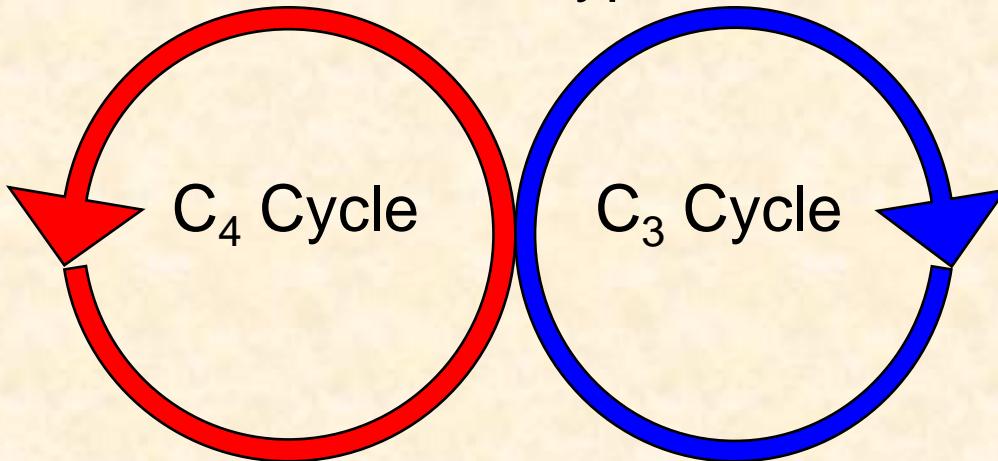




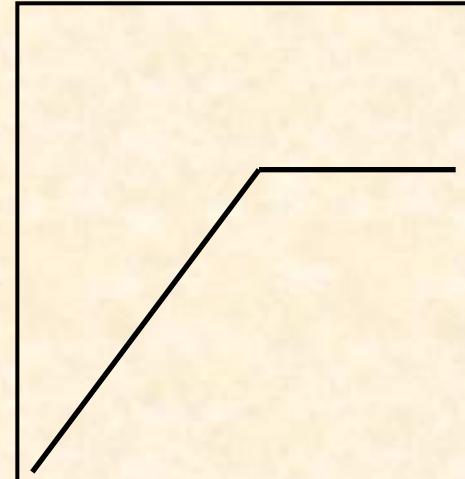
In *Flaveria bidentis*, control analysis using plants with an antisense Rubisco gene demonstrate that Rubisco exerts over photosynthesis is great at low temperature in  $\text{C}_4$  plants

From Kubien, von Caemmerer, Furbank and Sage (2003) Plant Physiology 132: 1577

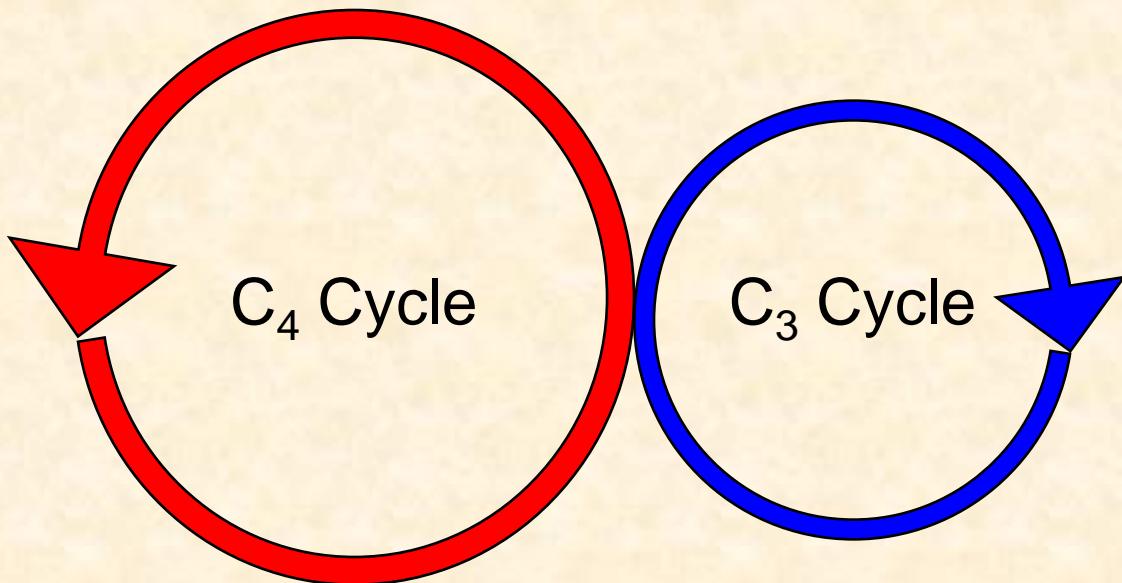
Normal Type



Photosynthesis



High PEP Carboxylase Type



Photosynthesis

