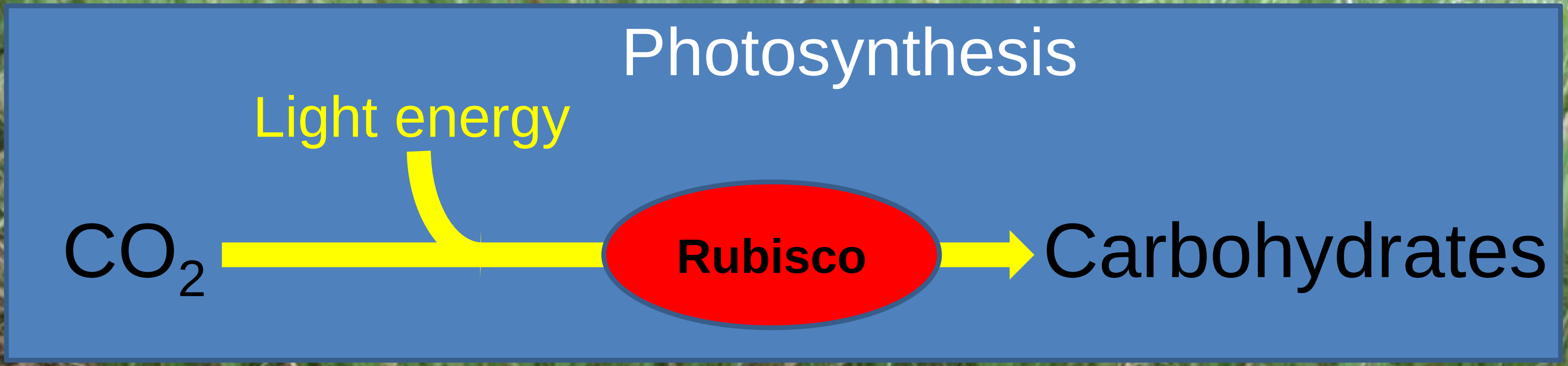
How Will Photosynthesis Change in Response to Global Warming



Photosynthesis

Light energy

CO_2 → **Rubisco** → Carbohydrates

Rubisco = Ribulose bisphosphate carboxylase/oxygenase

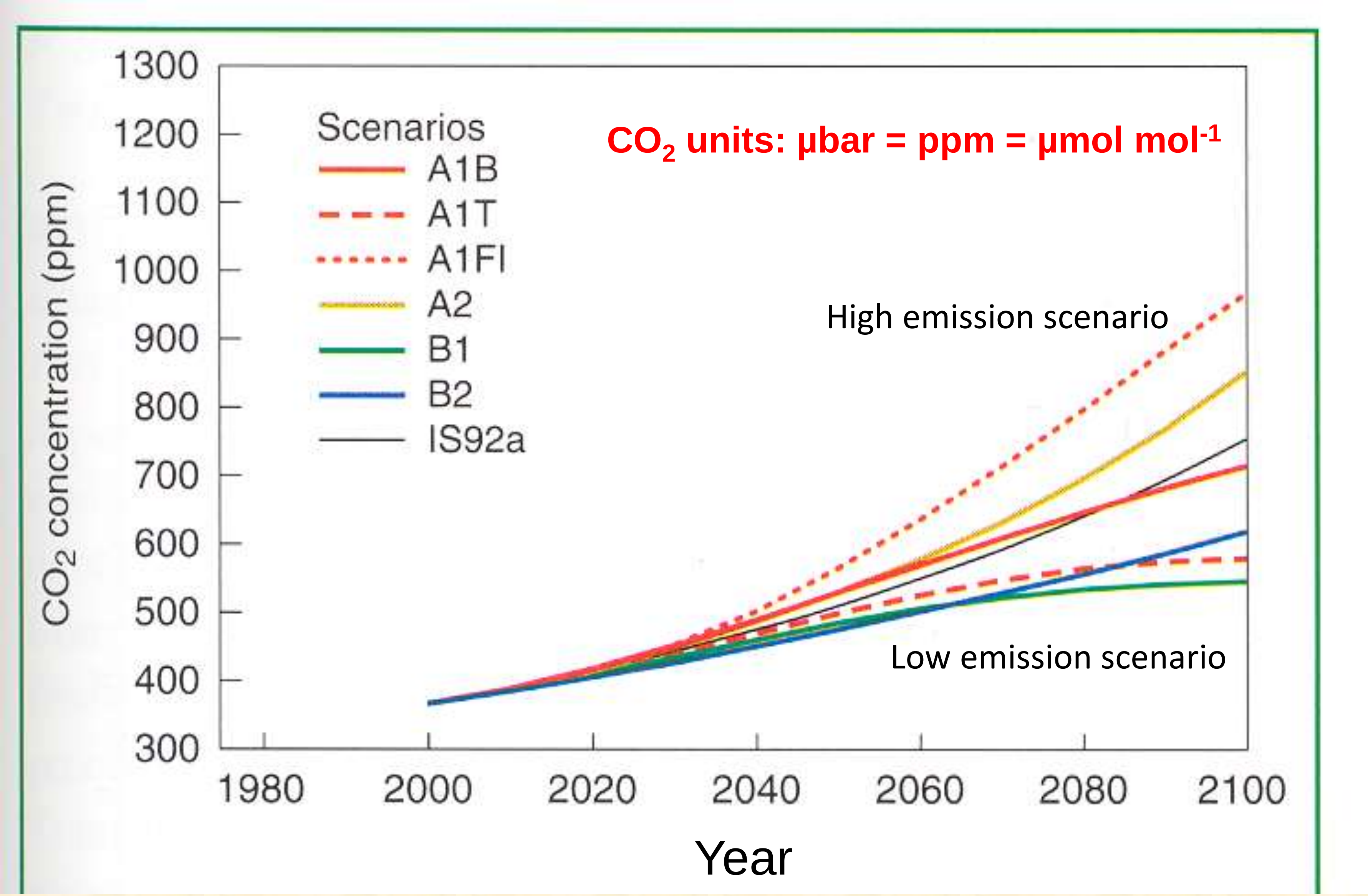
Rowan F. Sage
University of Toronto
25 Willcocks Street, Toronto, ON M5S3B2 Canada

Global Warming
(Global Change)

- Climate change
  - Climate warming
  - Altered precipitation regime
- Rising atmospheric CO_2
- Increasing ground level ozone
- Nutrient eutrophication
- Land use change

Modeled Greenhouse Gas Concentrations for 2000 to 2100

IPCC (2001) Climate Change 2001, Synthesis Report.
Cambridge University Press



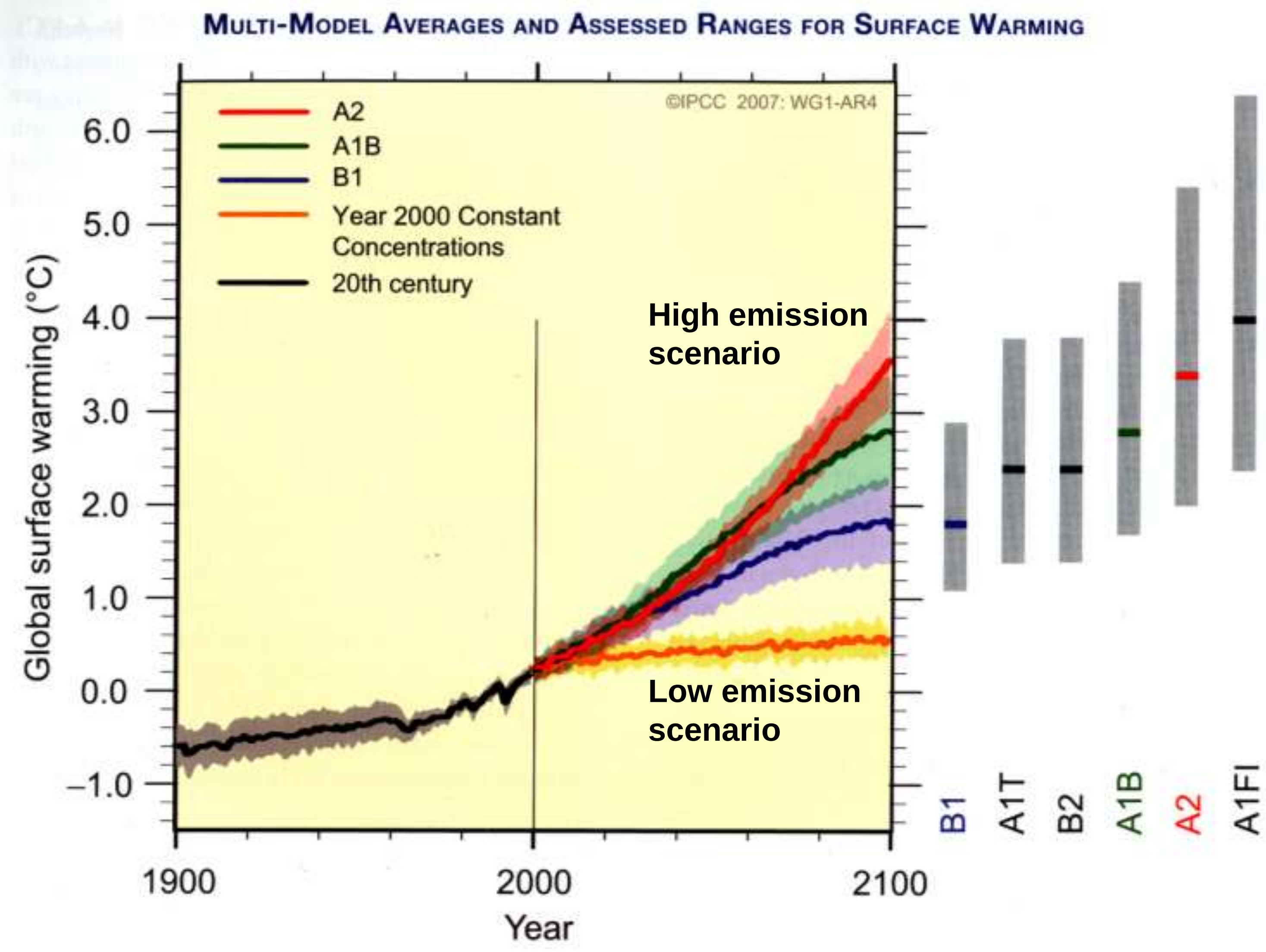
CO_2 units: μbar = ppm = μmol mol^{-1}

High emission scenario

Low emission scenario

Year

Global Temperature Change and Modeled Predictions: 1900 to 2100



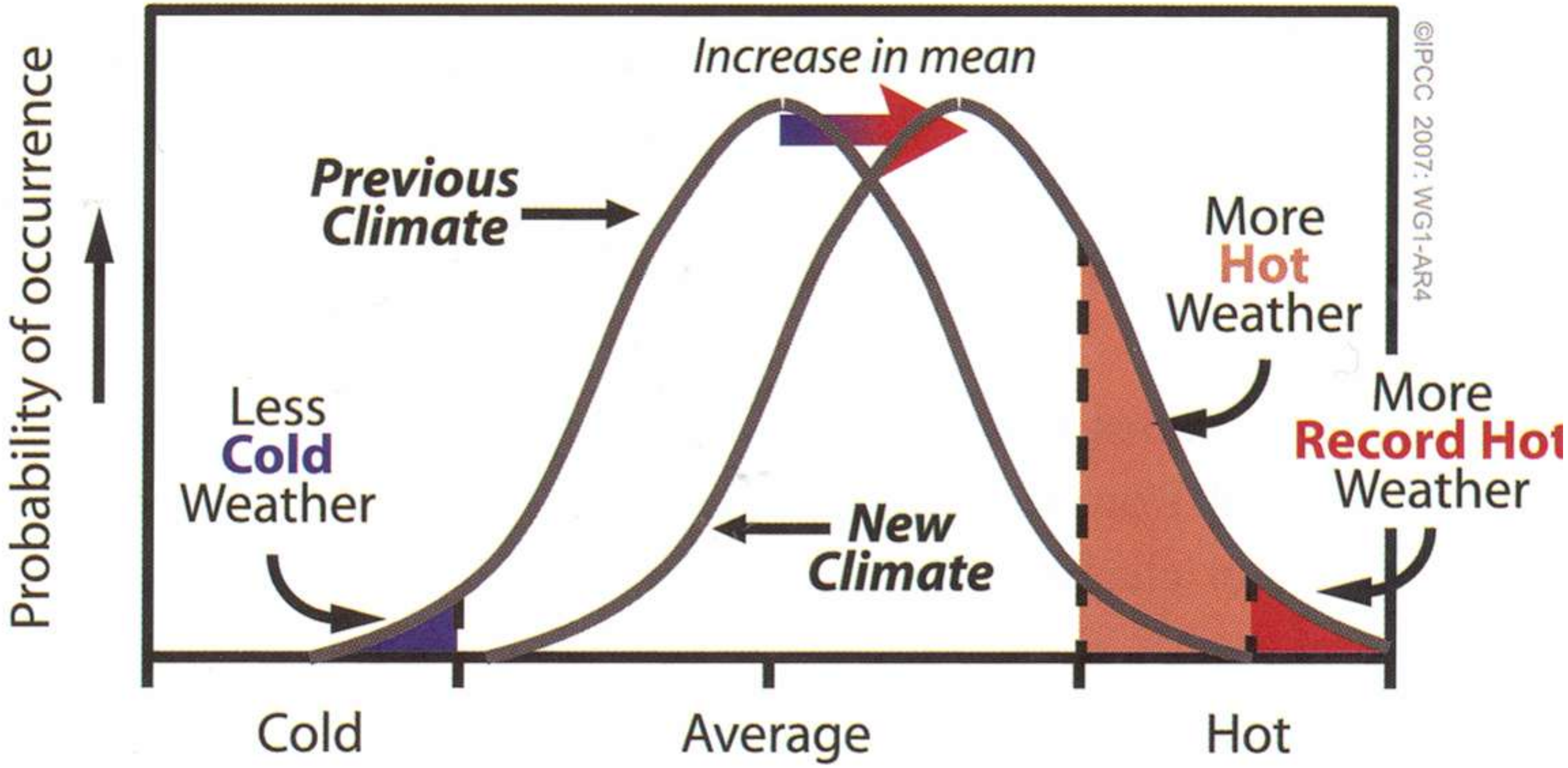
High emission scenario

Low emission scenario

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

Climate Warming is Not Just an Increase in Mean Temperature

A Schematic of How Warming Affects Climate



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

Climate Change and Photosynthesis

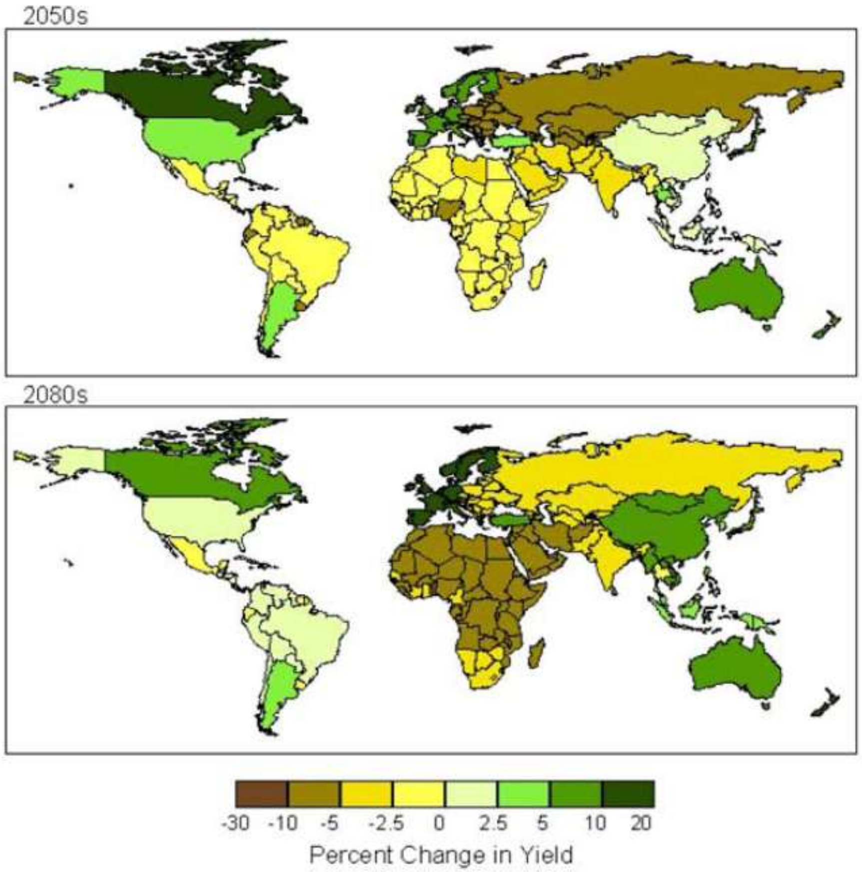
- Climate Warming
  - Mean change
  - Change in day versus night means
  - Regional change, high versus low latitude
  - Seasonal change, e.g. early versus mid-season
  - Change in heat event frequency and magnitude
  - Reduced magnitude and frequency of cold events
  - Occurs in an environment of elevated atmospheric CO_2

- Precipitation change
  - Mean change
  - Seasonal timing of change
  - Extreme event magnitude and frequency
    - Severe droughts
    - Flooding

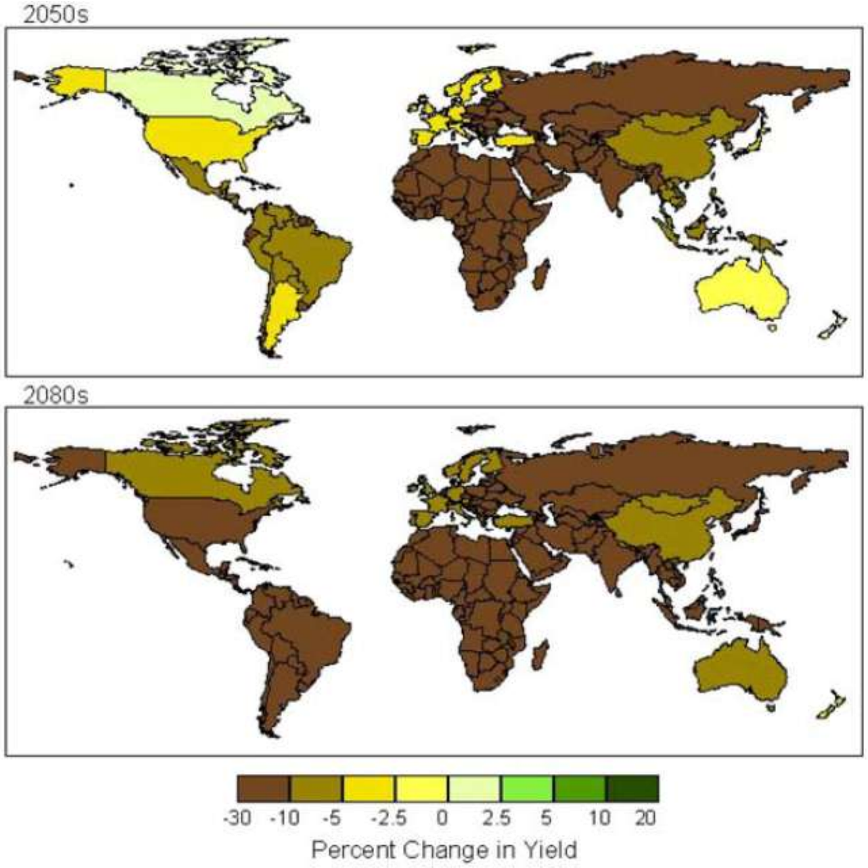
Modelled Change in Cereal Yield Assuming the A2a High Emission Scenario, Relative to 1990 Yields

Parry et al. (2004) *Global Environ. Change* 14:53-67

With physiological CO_2 effects



No physiological CO_2 effects



Yield reductions are due to increases in drought frequency and severity, and heat stress

Growth Chambers and Greenhouses

Open-Top Chambers for Field Work (1990's)


Swiss Calcareous Grassland

Tall grass prairie, Kansas


Chesapeake Bay Marsh


Tall grass prairie, Kansas

Terrestrial Plant Photosynthesis

- **C_3 plants**
  - Use the C_3 photosynthetic pathway
  - Suffer from photorespiration in warm environments
  - Operate below CO_2 saturation, so CO_2 responsive
  - Bioenergy examples: Arundo, willow, poplar, Eucalypts, Camelina
- **C_4 Plants**
  - Use the C_4 photosynthetic CO_2 concentrating mechanism
  - Minimal photorespiration
  - Low response to rising CO_2
  - Examples: maize, sorghum, sugar cane, Miscanthus, Napier grass
- **CAM plants**
  - Crassulacean Acid Metabolism to concentrate CO_2 around Rubisco
  - stomata open at night, closed in day
  - Slow growth, but very high water use efficiency
  - Examples: Agave, Euphorbia, Opuntia cacti

Terrestrial Plant Bioenergy Photosynthesis

C_3 Photosynthesis

Eucalyptus

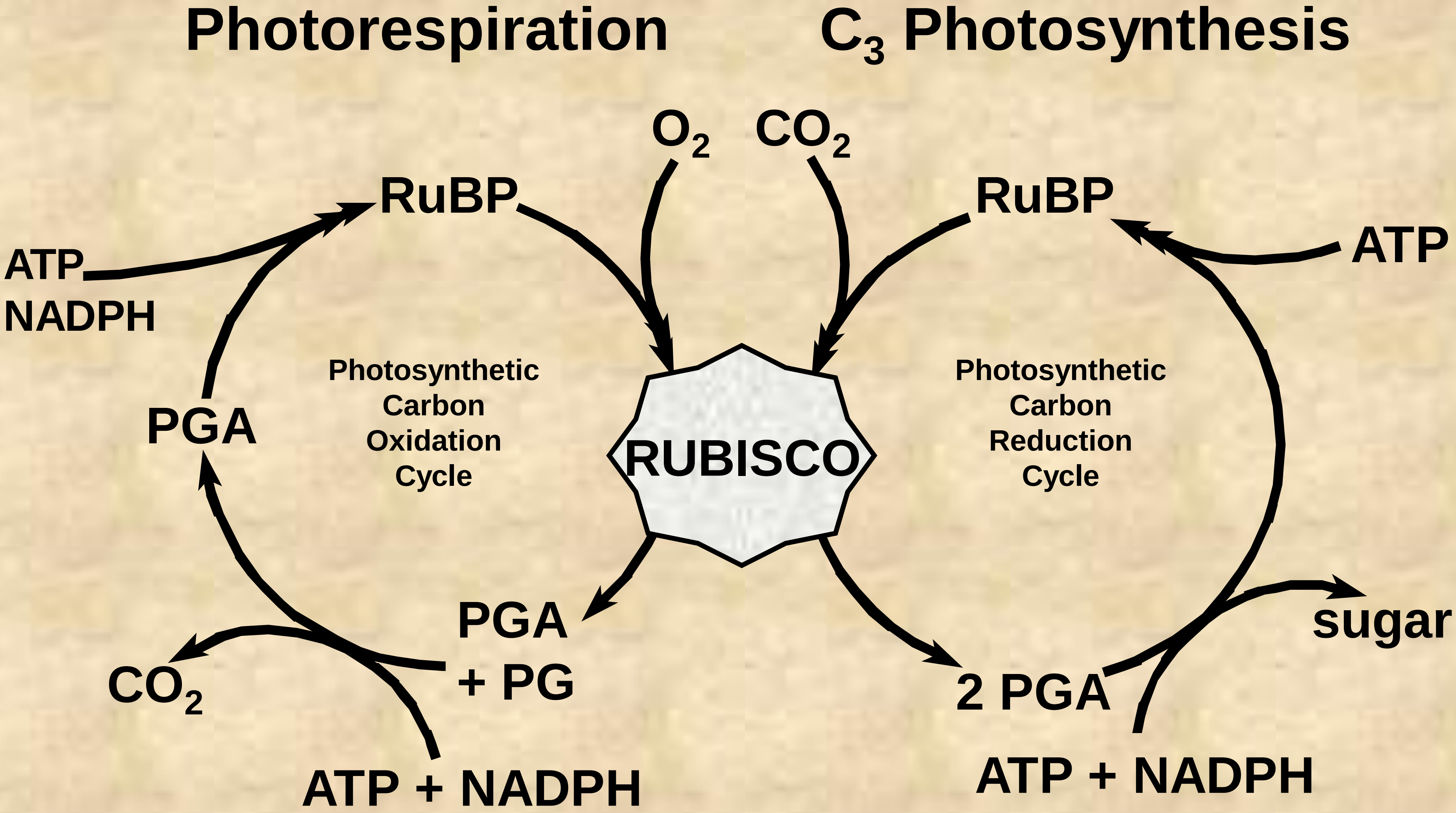
C_4 Photosynthesis

Sugar Cane

CAM Photosynthesis

Agave

THE DUAL CATALYTIC NATURE OF RUBISCO



Photorespiration

C_3 Photosynthesis

O_2

CO_2

RuBP

ATP
NADPH

PGA

Photosynthetic
Carbon
Oxidation
Cycle

RUBISCO

PGA
+ PG

CO_2

ATP + NADPH

RuBP

ATP

Photosynthetic
Carbon
Reduction
Cycle

2 PGA

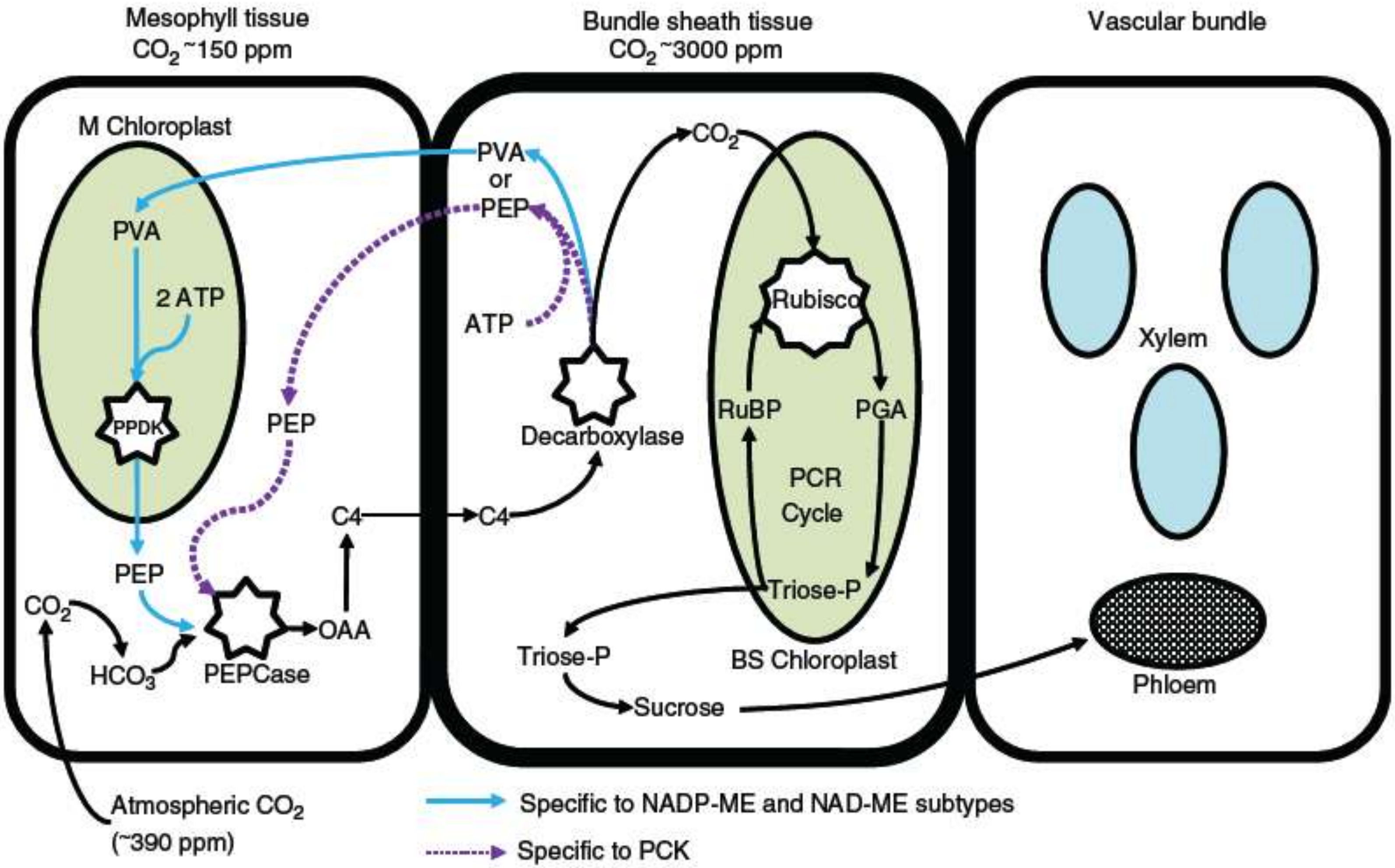
sugar

ATP + NADPH

Abbreviations: PG – phosphogylcolate; PGA - phosphogylcerate; RuBP - ribulose bisphosphate; Rubisco - RuBP carboxylase/oxygenase

A Schematic of C_4 Photosynthesis

Sage RF, Sage TL. (2013) C_4 Plants. *In* Levin S.A. (ed.) Encyclopedia of Biodiversity, second edition, Volume 2. : Academic Press, pp. 361-381.

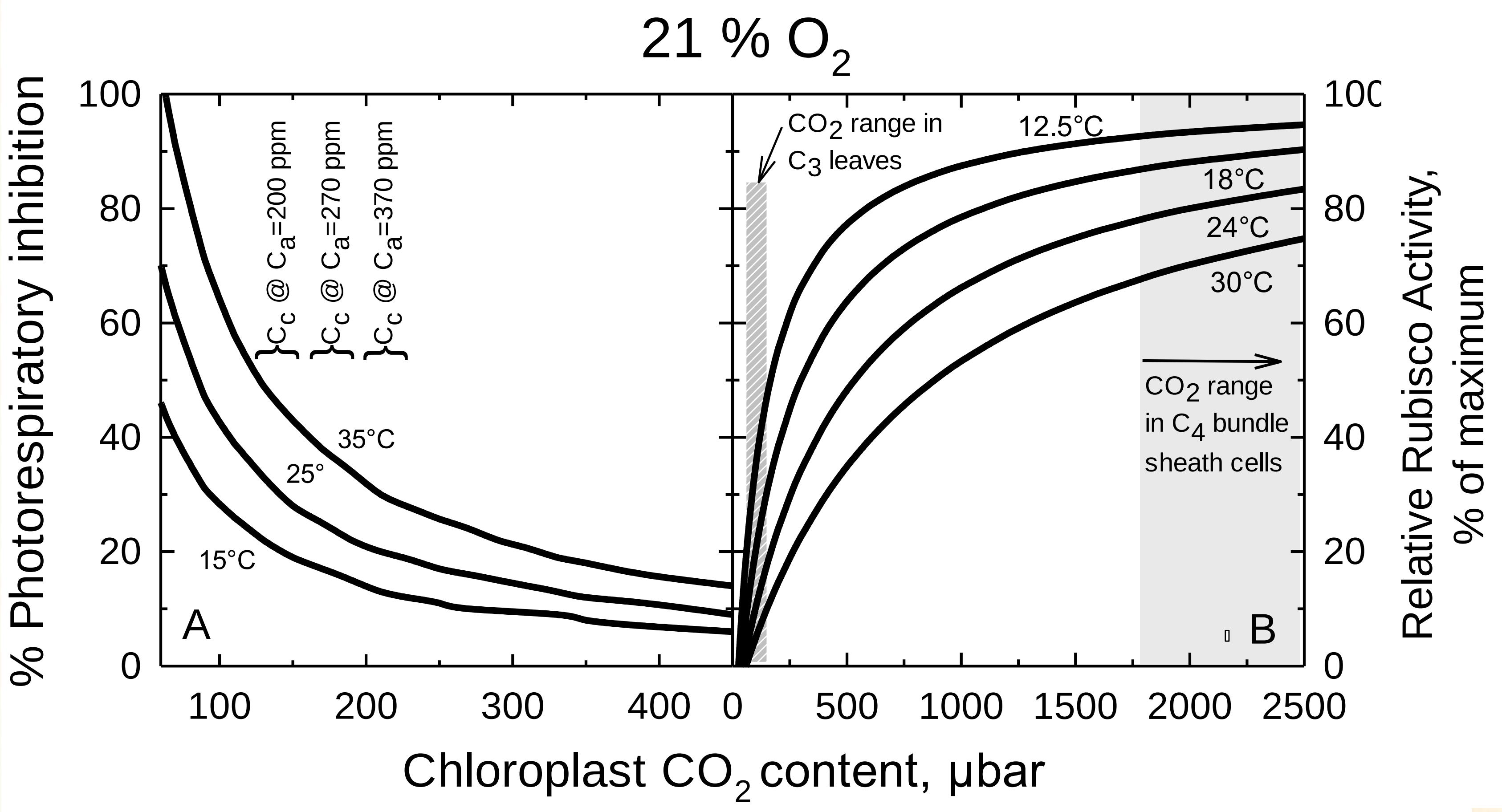


Abbreviations: PEP, phosphoenolpyruvate; PEPCase, PEP carboxylase; PPDK, pyruvate phosphate dikinase; PVA, pyruvate; PCR, photosynthetic carbon reduction cycle.

The Effect of CO_2 Concentration on Rubisco Function

% Photorespiratory Inhibition

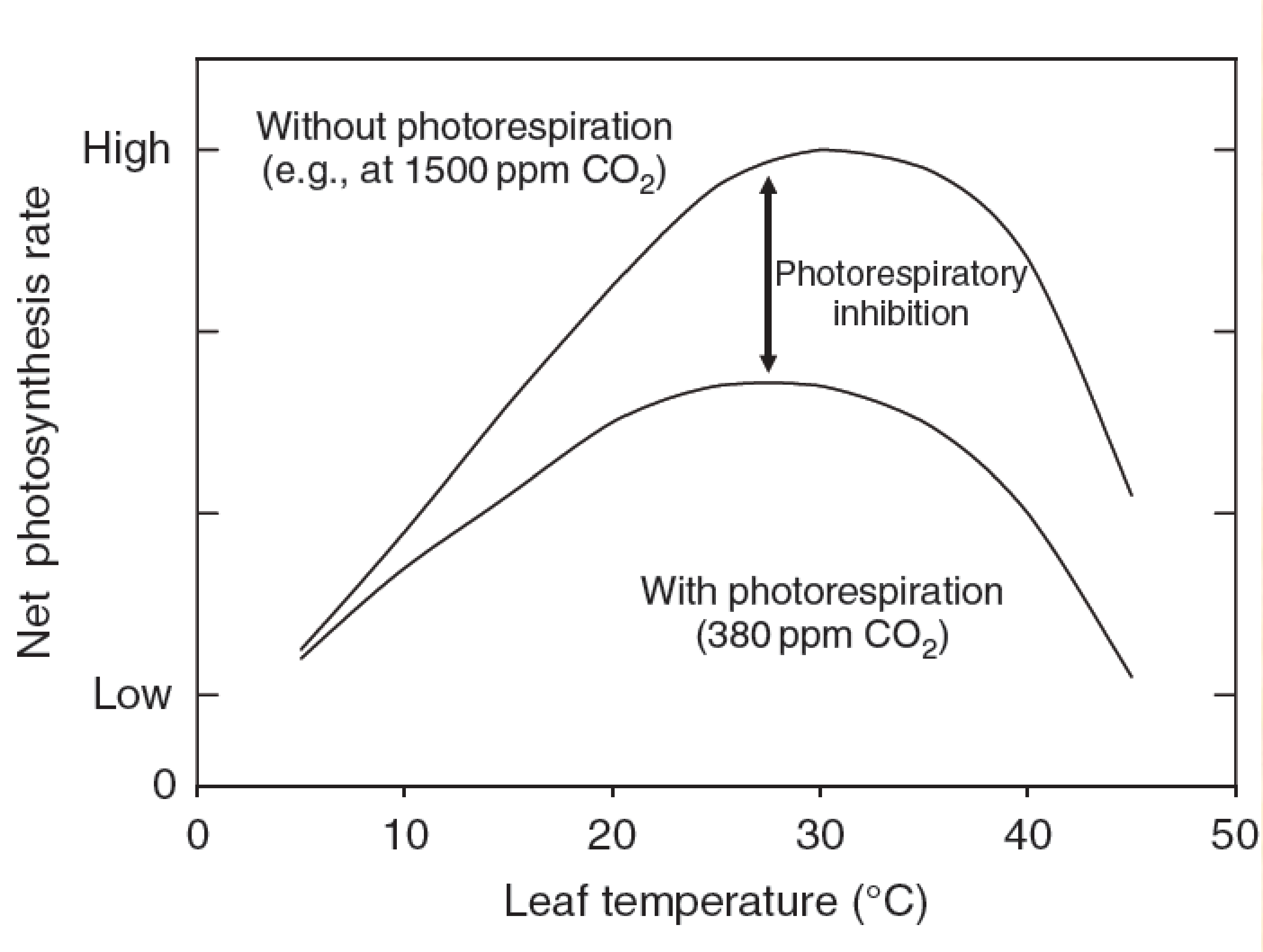
Relative Rubisco Activity



Sage RF, Sage TL. (2013) C_4 Plants. *In* Levin S.A. (ed.) Encyclopedia of Biodiversity, second edition, Volume 2. : Academic Press, pp. 361-381.

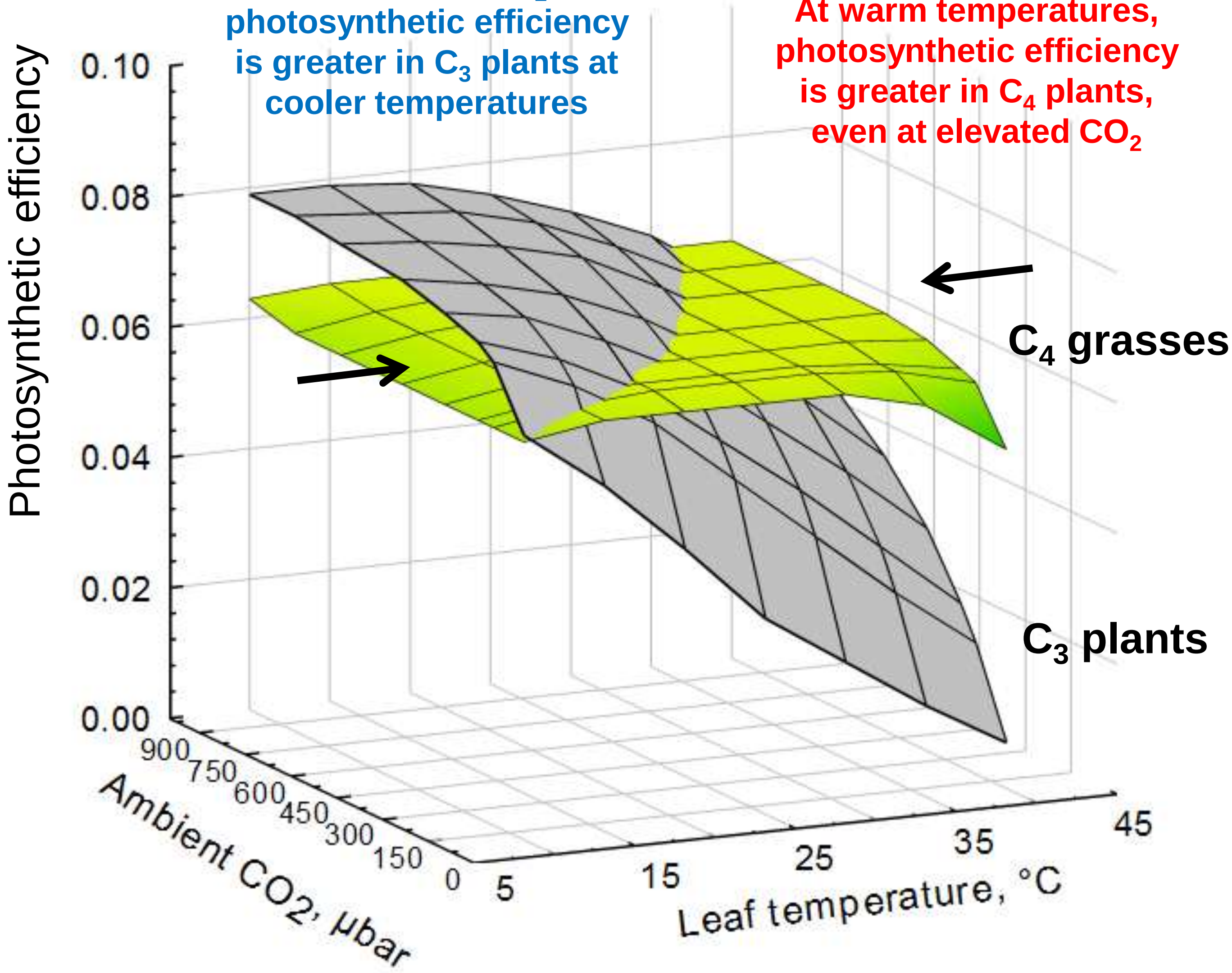
The Temperature Response of C_3 Photosynthesis with and without Photorespiration

Sage RF (2007) Autotrophs. *In* Sorgensen SE, Fath BD, *eds*. *Encyclopedia of Ecology*. Elsevier. Oxford, UK. pp. 291-300.



Efficiency of C_3 and C_4 Photosynthesis as a Function of CO_2 and Temperature

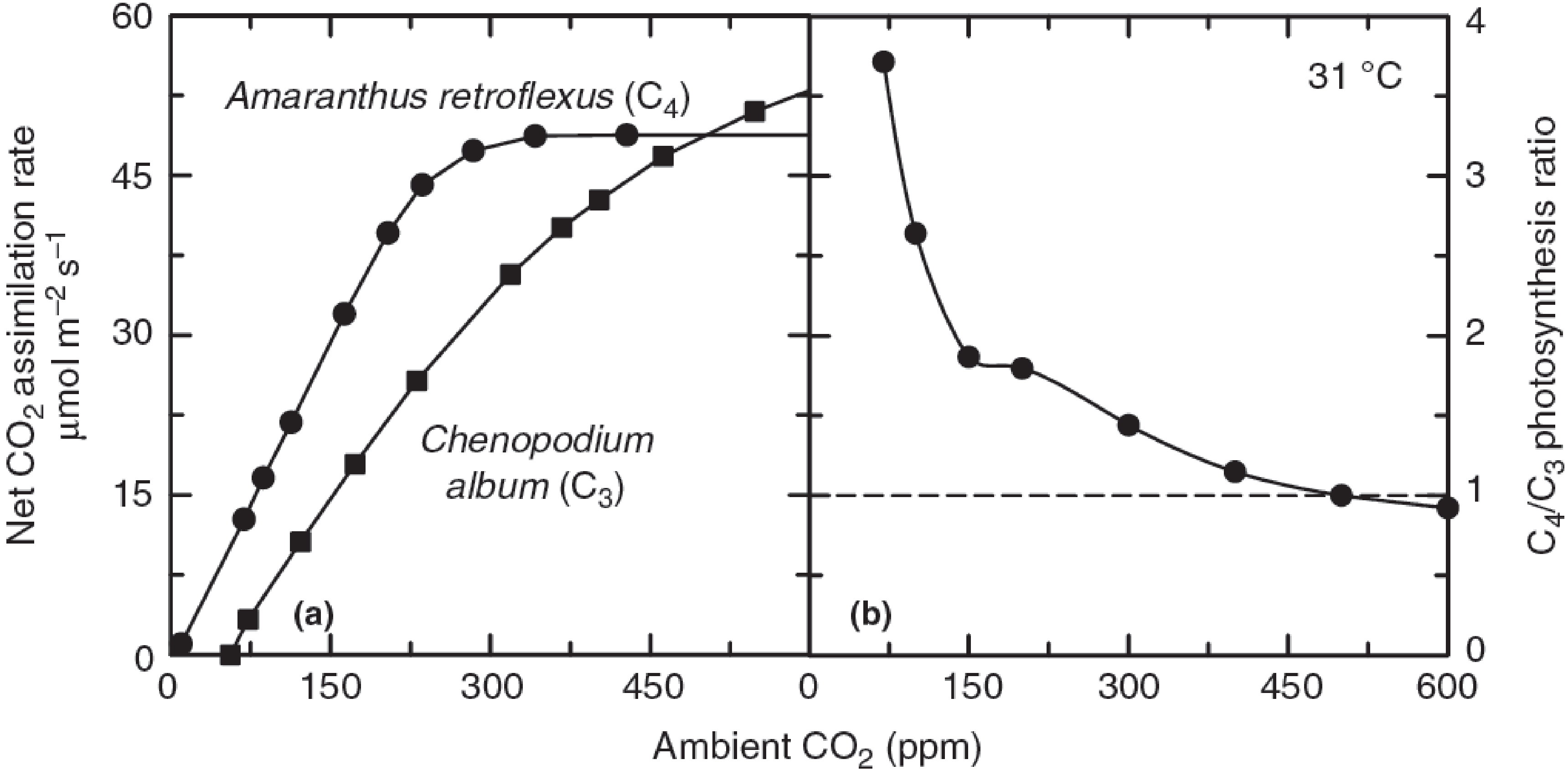
Modelled using the WIMOVAC photosynthesis program . From Sage RF (2000) *In* Sheehy JE, Mitchell PL, Hardy B, *eds*. *Redesigning Rice Photosynthesis to Increase Yield.* International Rice Research Institute, Manila, The Philippines. 13-38.



At elevated CO_2, photosynthetic efficiency is greater in C_3 plants at cooler temperatures

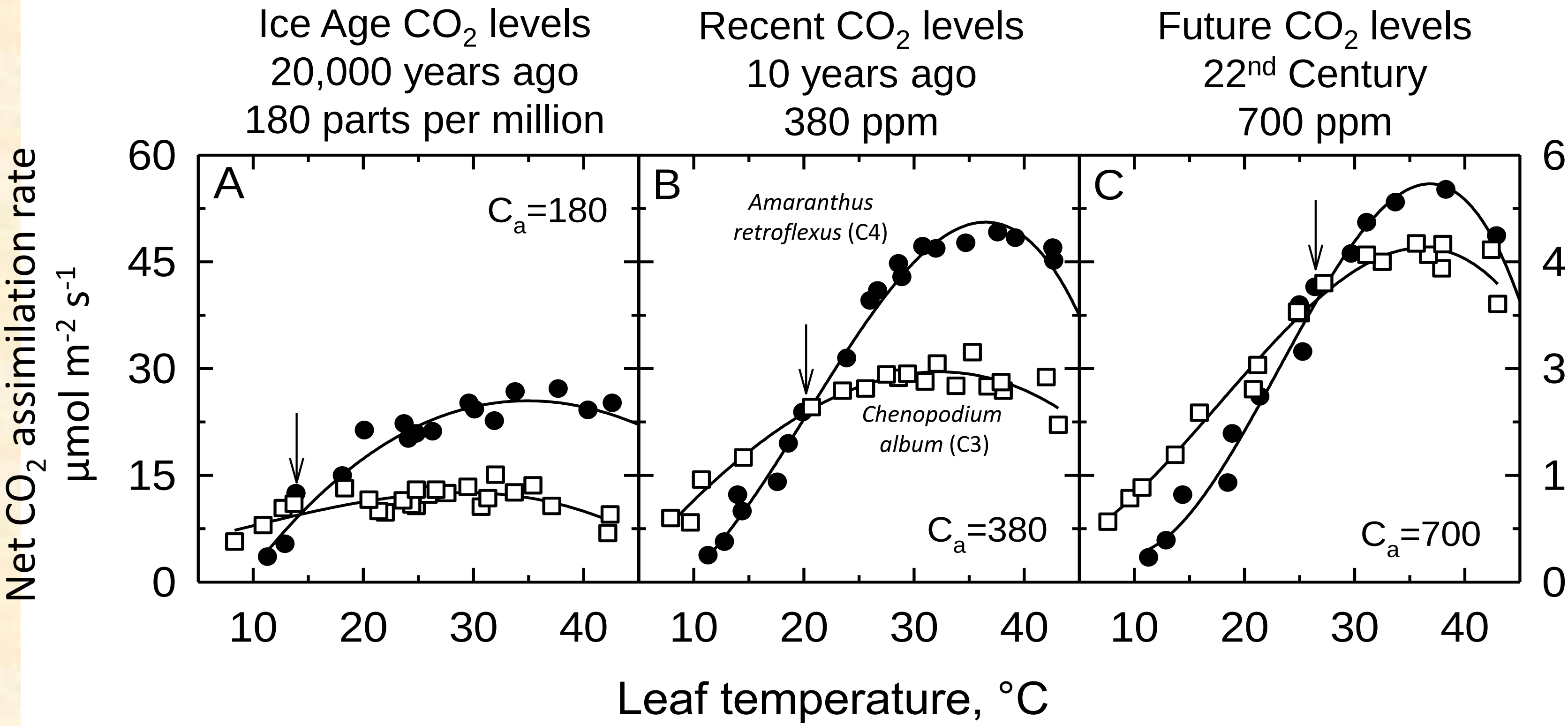
At warm temperatures, photosynthetic efficiency is greater in C_4 plants, even at elevated CO_2

The Response of C_3 and C_4 Photosynthesis to Intercellular CO_2 Concentration



Sage RF, Sage TL. (2013) C_4 Plants. *In* Levin S.A. (ed.) Encyclopedia of Biodiversity, second edition, Volume 2. : Academic Press, pp. 361-381.

The Temperature Response of C_3 and C_4 Photosynthesis at Three Atmospheric CO_2 Concentrations



From: Sage RF, Pearcy RW (2000) The physiological ecology of C_4 photosynthesis. *in* R.C. Leegood, Sharkey TD, von Caemmerer S, *Photosynthesis: Physiology and Metabolism. eds*. Kluwer Academic. Dordrecht. pp. 497-532

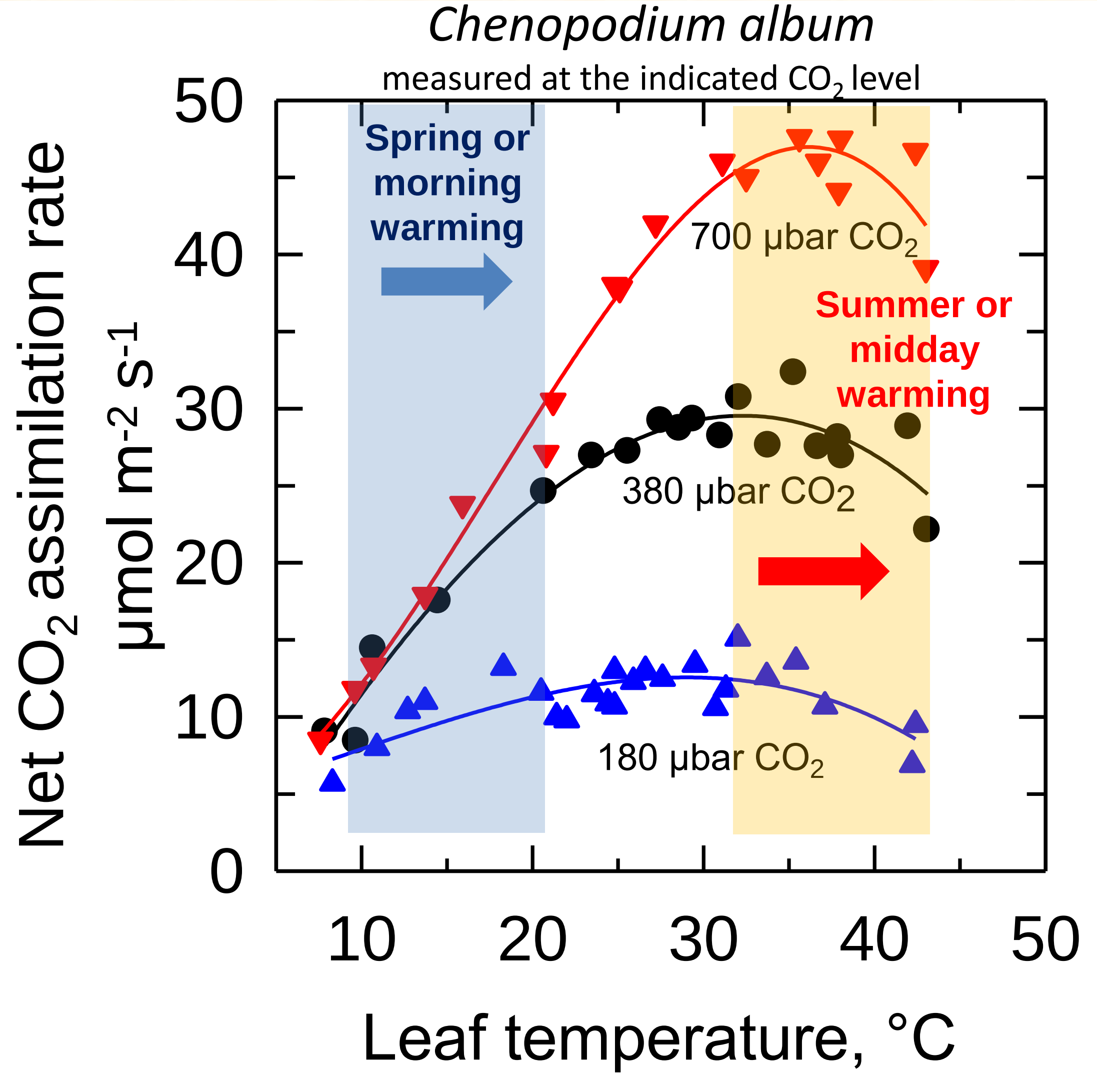
The Context of the Photosynthetic Response to Global Change Is Important

I. Geographic scale

- A) Cold versus warm location
- B) Dry versus wet location

An Example of How Seasons Can Affect the Response to Climate Warming

The Temperature Response of C_3 Photosynthesis



Chenopodium album

measured at the indicated CO_2 level

Cool season warming:

- **stimulates *A***
- **low CO_2 responsive**

Hot season warming

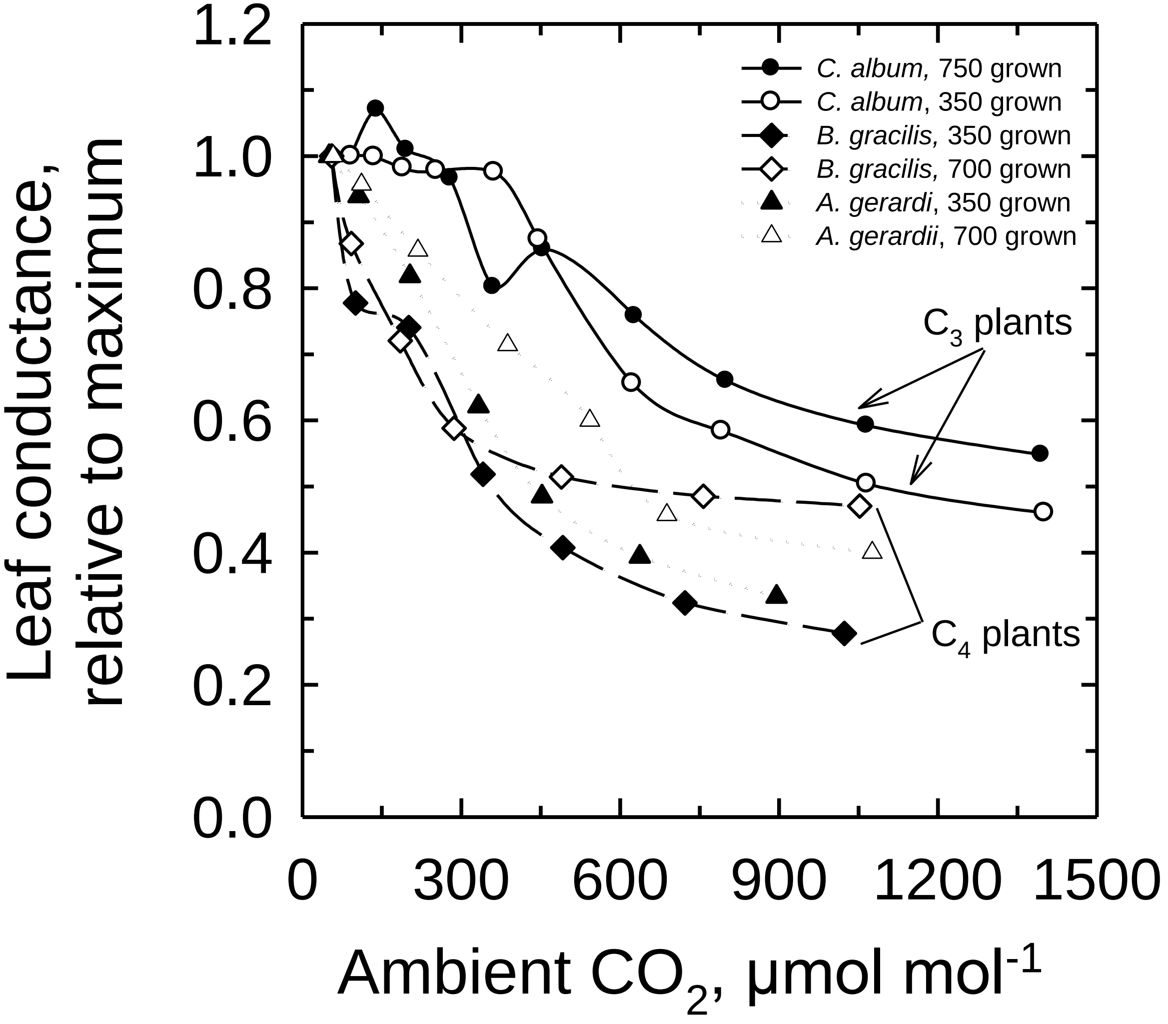
- **inhibits *A***
- **high CO_2 responsive**

Adapted from from: Sage RF, Pearcy RW (2000) The physiological ecology of C_4 photosynthesis. *in* R.C. Leegood, Sharkey TD, von Caemmerer S, *Photosynthesis: Physiology and Metabolism. eds*. Kluwer Academic. Dordrecht. pp. 497-532

Rising CO_2 Reduces Stomatal Conductance

Rising CO_2 induces partial stomatal closure, and hence reduces transpiration

Lower stomatal
conductance means
less open stomata
= reduced
transpiration



Sage R.F. and Kubien D. (2003) Photosynthesis Research 77: 209-225.

Soil Water Content in Response to CO_2 gradient

C_3 and C_4 mixed grassland

Polley et al. (2002) Global Change Biology 8: 1118-1129

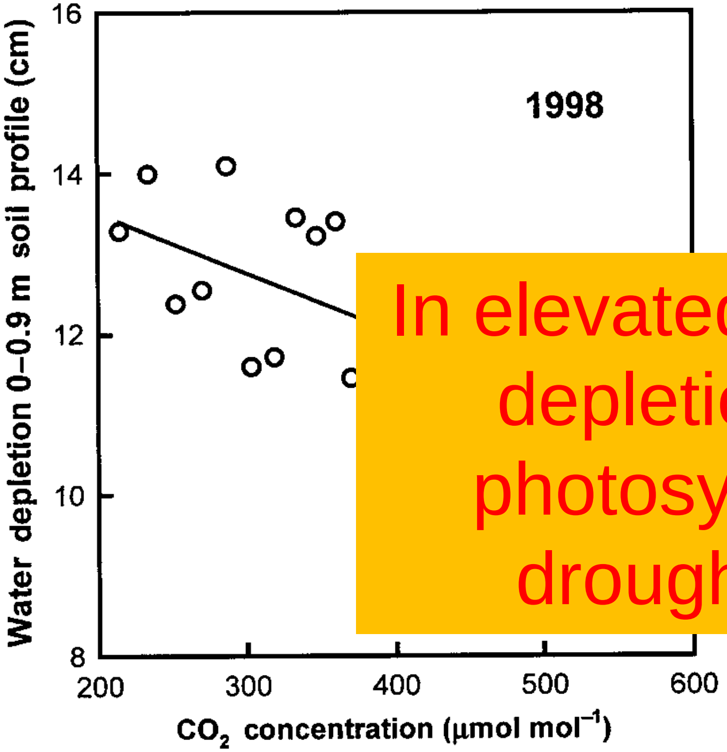
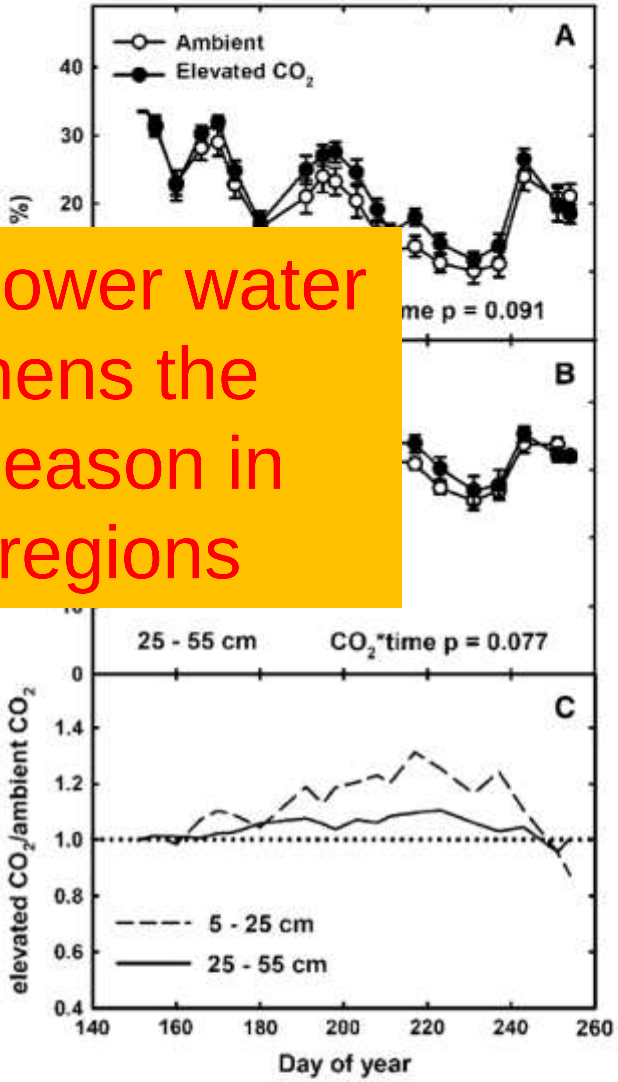


Fig. 5 Maximum depletion of soil water to 0.9 m depth during 1998 in a C3/C4 grassland exposed to subambient to superambient CO_2 concentrations. Water depletion in each of the 5 m^2 compartments of grassland in CO_2 chambers was calculated by subtracting the average minimum water content of each soil profile from the average maximum water content following initiation of CO_2 control each year (each mean is the average of five measurements on consecutive weeks). The line was fit by linear regression ($r^2 = 0.49$, $P = 0.0005$).

Maize in the SOYFACE Facility

Leakey et al. (2006) Plant Physiol. 140:779-790



In elevated CO_2, slower water depletion lengthens the photosynthetic season in drought-prone regions

The Scale of the Photosynthetic Response Is Important

I. Geographic location

- A) Cold versus warm growth season
- B) Dry versus wet climate

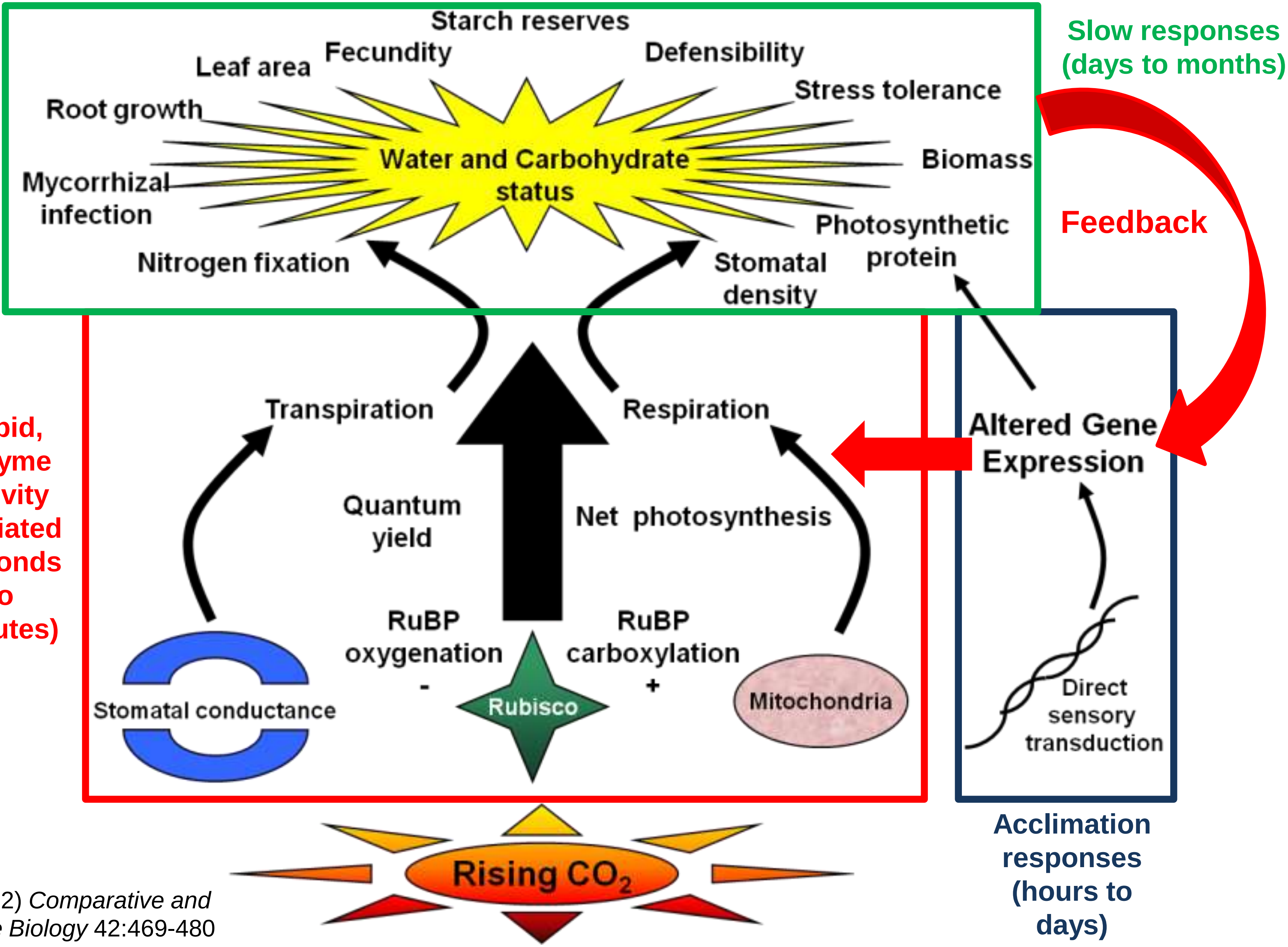
II. Plant Spatial Scale

- A) Cell to leaf
- B) Whole plant
- C) Crop canopy

III. Temporal Scale

- A) Short term enzyme mediated response (half time of seconds)
- B) Short-term regulatory response (a half time of minutes)
- C) Acclimation response (long-term phenotypic response)
- D) Adaptive (genotypic alteration) via natural artificial selection

Response Possibilities of Plants to Rising CO_2



Slow responses (days to months)

Feedback

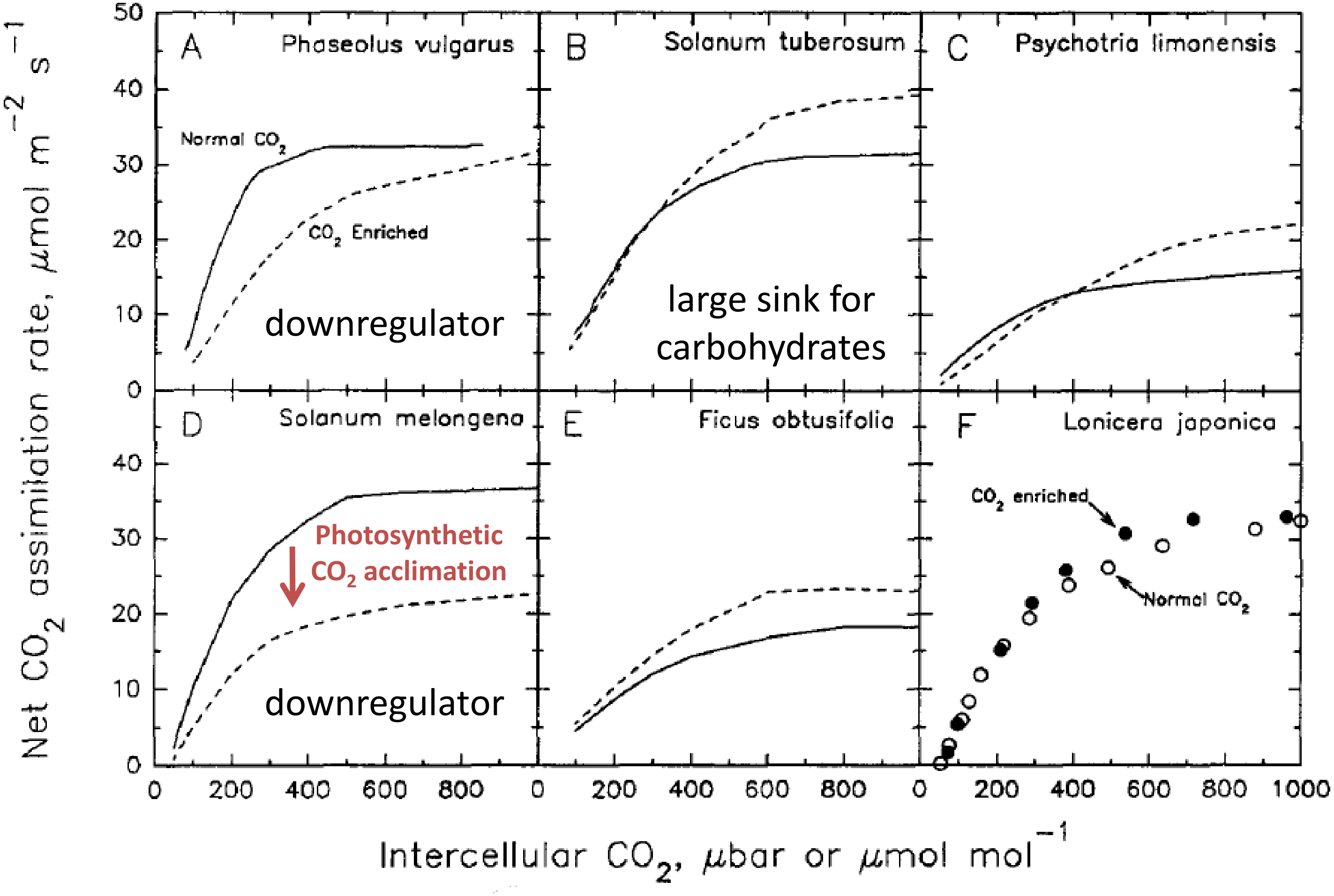
Rapid, enzyme activity mediated (seconds to minutes)

Acclimation responses (hours to days)

Sage (2002) *Comparative and Integrative Biology* 42:469-480

Photosynthetic Acclimation to High CO_2 in C_3 Plants

Responses of photosynthesis to varying measurement CO_2 for plants grown at current or elevated CO_2



downregulator

large sink for carbohydrates

Photosynthetic CO_2 acclimation

downregulator

Plants grown at elevated CO_2 show substantial variation in the photosynthetic stimulation by high CO_2.

Some species sustain the high CO_2 enhancement of photosynthesis.

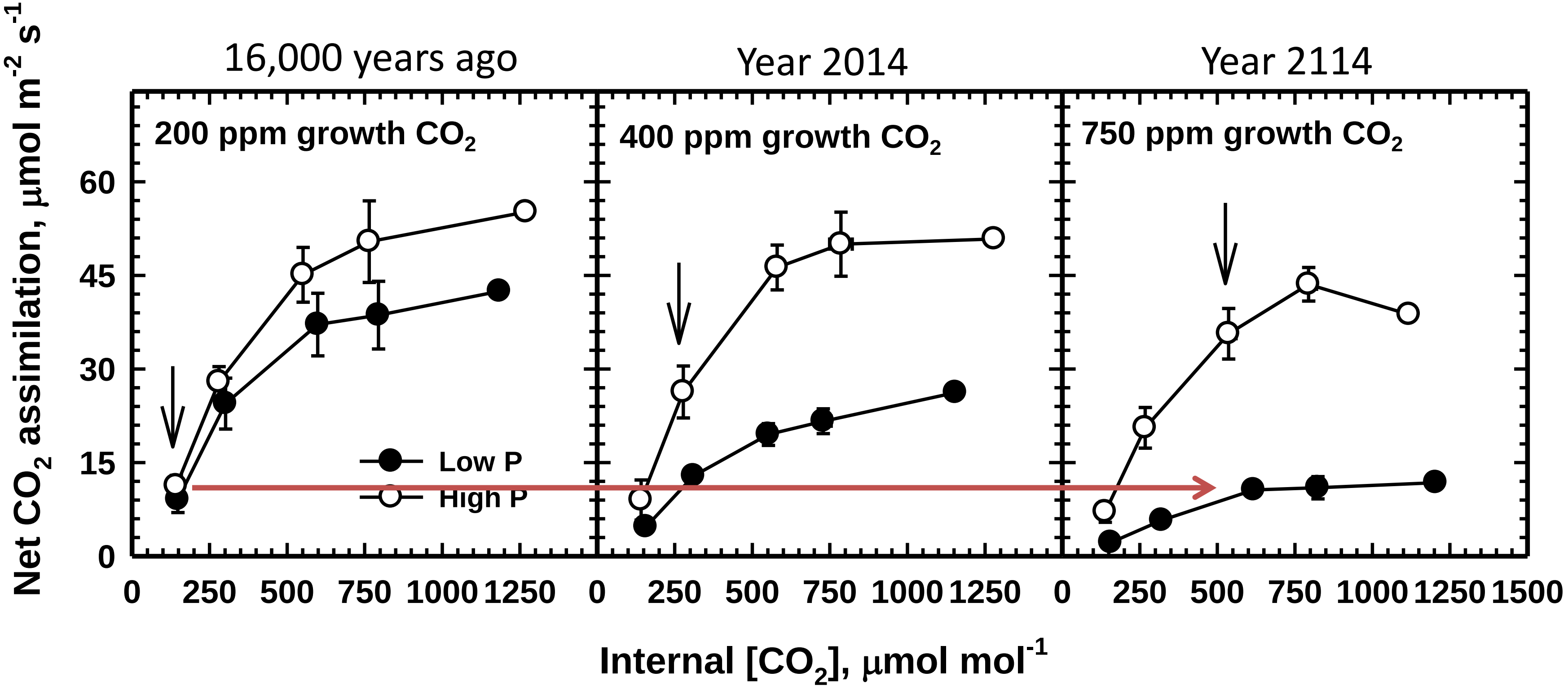
Others show downregulation and little long-term enhancement

Sage (1994) Photosynthetic acclimation to elevated CO_2. The gas exchange perspective. *Photosynthesis Research* 39:351-368

Nutrient Supply Modulates Photosynthetic Responses to Rising CO_2

White Lupine (*Lupinus albus*) grown at two phosphorous supply rates

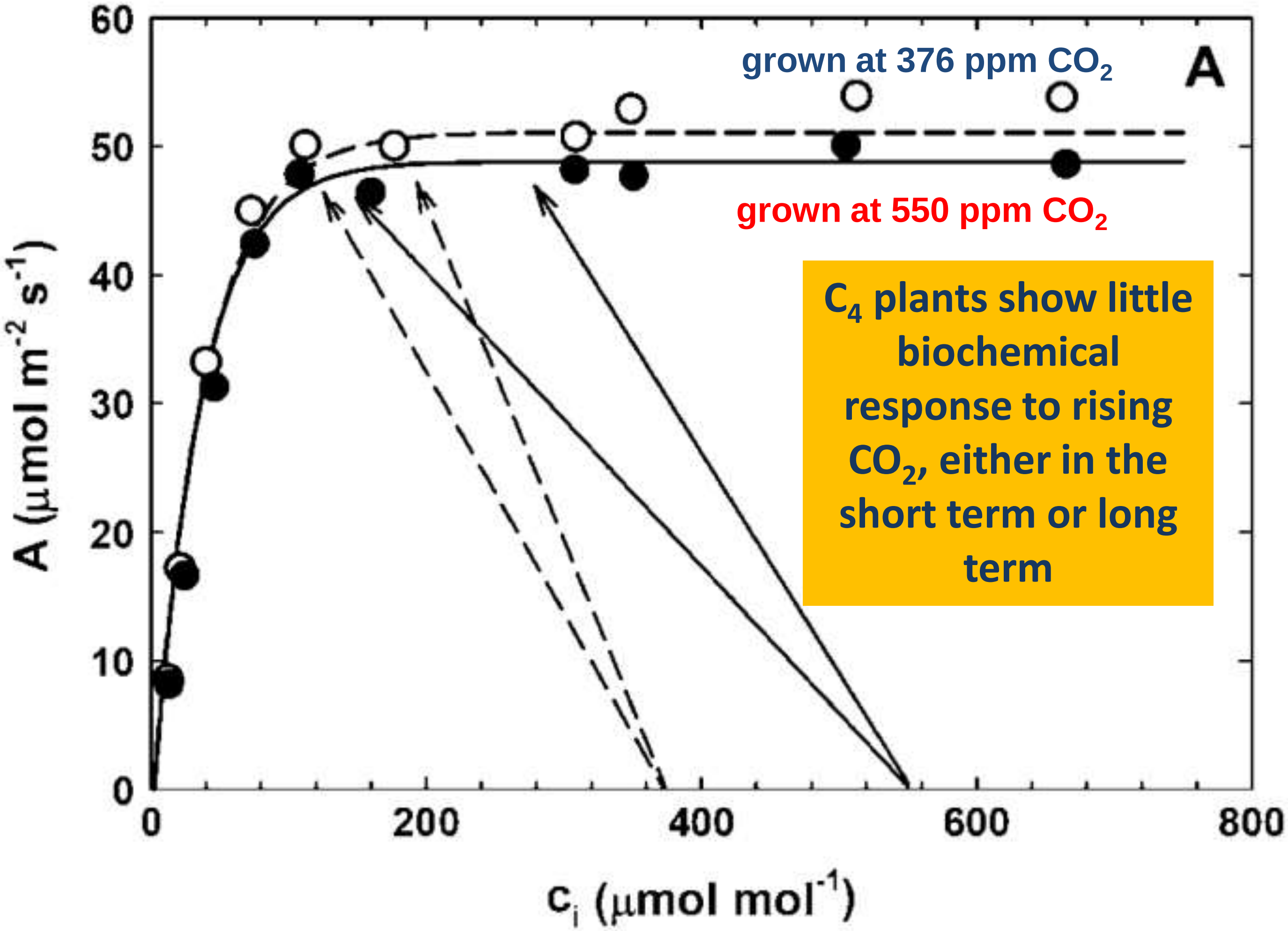
CO_2 enrichment above 200 ppm CO_2 does not stimulate photosynthesis if soil phosphorous is limiting



Campbell CD, Sage RF (2002) *Plant, Cell Environment* 25:1051-1059

High CO_2 Acclimation of C_4 Photosynthesis in Maize

Leakey et al. (2006) Plant Physiol. 140:779-790



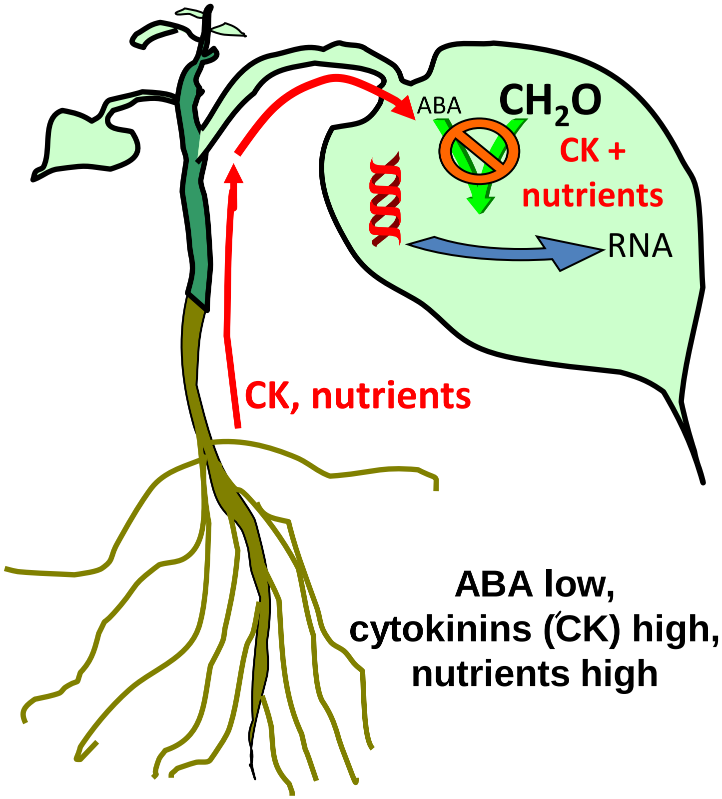
C_4 plants show little biochemical response to rising CO_2, either in the short term or long term

Net Photosynthesis Rate

Intercellular CO_2 partial pressure

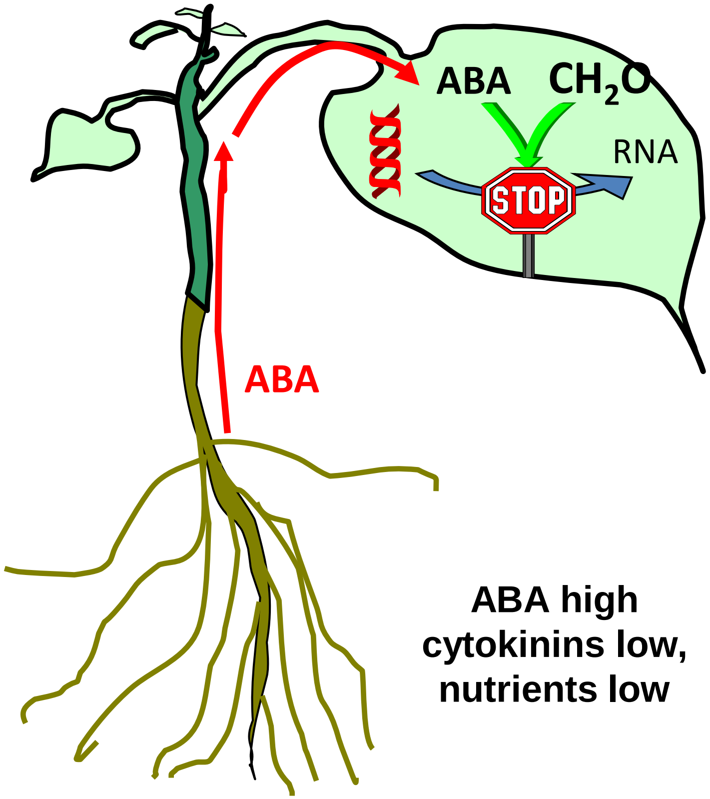
A Model for the CO_2 Acclimation Response

High Carbohydrate Levels in Plants Cause Feedback Signals that Reduce Expression of Photosynthetic Genes



ABA low,
cytokinins (CK) high,
nutrients high

Low Carbohydrate Roots
(for example, at low atmospheric CO_2)



ABA high
cytokinins low,
nutrients low

High Carbohydrate Roots
(for example, at high atmospheric CO_2)

Sage (2002) *Comparative and Integrative Biology* 42:469-480

Six Photosynthetic Lessons From High CO_2 FACE Experiments

Adapted from Leakey ADB, Ainswort EA, Bernacchi CJ, Rogers A, Long SP, Ort DR (2010) Elevated CO2 effe[illegible]en, and water relations: six important lessons from FACE. J. Exp Botany 10: 285[illegible]

Do not account for evolutionary or breeding responses to changing atmospheric CO_2

1. CO_2 uptake is enhanced by elevated [CO_2] despi[illegible] photosynthetic capacity. Median estimate are a [illegible]ulation.

2. Nutrient deficiency reduces long term [illegible] photosynthesis.

3. The nitrogen use efficiency o[illegible]ced about 30% at high CO_2, leaf nitrogen declines[illegible]

4. Water use declin[illegible]nd canopy scales, delaying the onset of drought. This[illegible]mportant in warm, dry climates.

5. In C[illegible]ulation of photosynthesis by a doubling of growth CO_2 [illegible] primary observed when water supply is deficient.

6. Grow[illegible]esponses to elevated CO_2 are generally less than photosynthetic responses. This leads to excess carbon in the plant that is stored, excreted or metabolically. disrupts the plant function. (Plants are sink limited in elevated CO_2).

Adaptation Considerations

1) Current crops are not adapted to elevated CO_2 but can be via breeding and genetic engineering.
2) Different crops varieties are adapted to different temperature ranges.
3) Crop photosynthesis in the future will be determined in part by crop improvement strategies

Some Crop Improvement Options

- Increase Sink Capacity
- Improve Nitrogen Use efficiency in elevated CO_2:
  - In C_3 plants by reducing Rubisco investment.
  - In C_4 plants by reducing investment in the C_4 metabolic cycle.

Summary of Key Points

- C_3 photosynthesis will respond more to rising CO_2 at elevated temperature than at cool temperature.

- C_4 photosynthesis has a weak response to rising CO_2 above current levels, but is strongly stimulated by warming temperatures up to near 35°C.

- Climate warming will enhance photosynthesis in cool settings, but in warm settings could push leaves above their thermal optimum.

- Human improvement of crops will influence the eventual photosynthetic response to global climate change in bioenergy production systems.

References

ADB Leakey, EA Ainsworth, CJ Bernacchi, A Rogers, SP Long & DR Ort (2009) Elevated CO_2 effects on plant carbon, nitrogen and water relations: six important lessons from FACE. Journal of Experimental Botany 60(10): 2859-2876.

Long SP, Ort DR (2010) More Than Taking the Heat: Crops and Global Change. Current Opinion in Plant Biology13: 241-248.

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Sage RF, Peixoto M, Sage TL (2014) Photosynthesis in sugarcane. *In* Moore PH , Botha F, eds. *Physiology of Sugarcane*. Wiley and Sons, Inc. Oxford pp. 121-154.