Problems with C3 photosynthesis

Increase in photorespiration - in hot dry conditions

Why? - Competition between O_2 and CO_2 for Rubisco binding site

Photorespiration increases when

$[O_2]$ / $[CO_2]$ inside the leaf increases

Photosynthetic Pathway Variation

- Focus until now has been on C3 photosynthesis
- Variation in biochemistry of photosynthesis exists and has ecological implications – CAM and C4 photosynthesis

Biochemistry worked on by Hatch and Slack 1966

C4 and CAM are two evolutionary solutions to the problem of maintaining photosynthesis with stomata partially or completely closed on hot, dry days

(Carbon Concentrating Adaptations)

Photosynthetic Pathway Variation

- **C3** – CO_2 fixation by Rubisco; PGA (phosphoglycerate – a 3 carbon sugar) is the product of initial carboxylation
- **C4** – CO_2 fixation by PEP carboxylase to produce OAA (oxaloacetate – a 4 carbon acid); C4 then transported within the leaf, decarboxylation and re-fixation by Rubisco.
- **CAM** (crassulacean acid metabolism) – CO_2 fixation by PEP carboxylase to OAA, <u>but results in the production of malic acid in the vacuole during the day and de-carboxylation and fixation at night</u>

C3, C4 and CAM

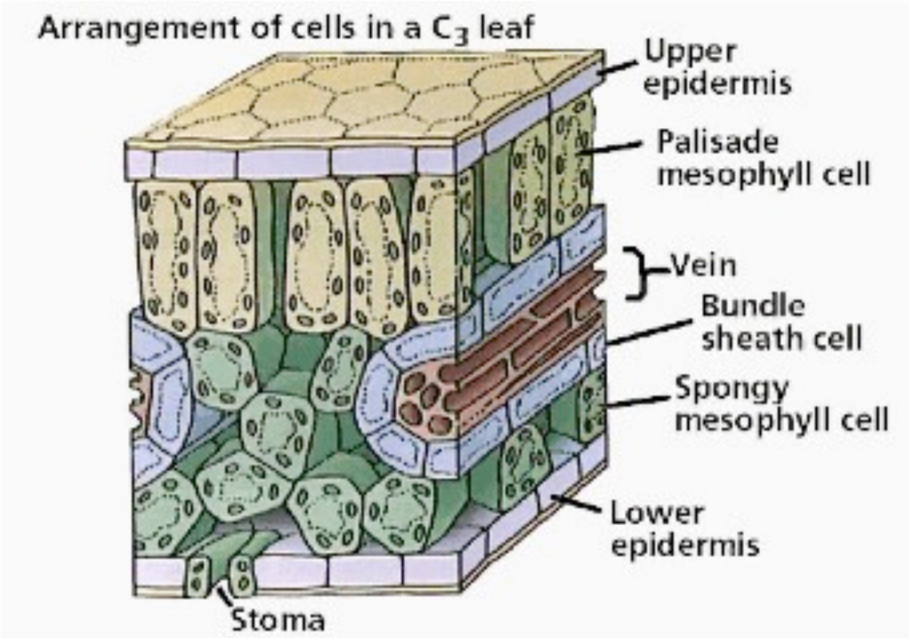
- C4 photosynthesis results in CO_2 concentrating at the site of carboxylation, by a <u>spatial specialization</u> of biochemistry
  - ***Kranz Anatomy***

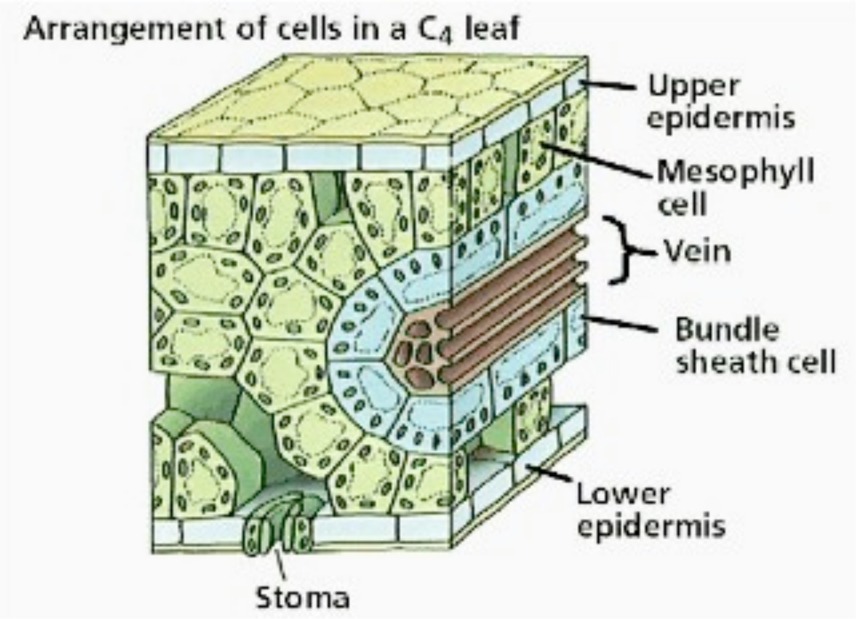
(Bundle Sheath Design)

- CAM photosynthesis results in CO_2 concentration at the site of carboxylation by a <u>temporal specialization</u> of biochemistry

Anatomical differences between C3 and C4 plants

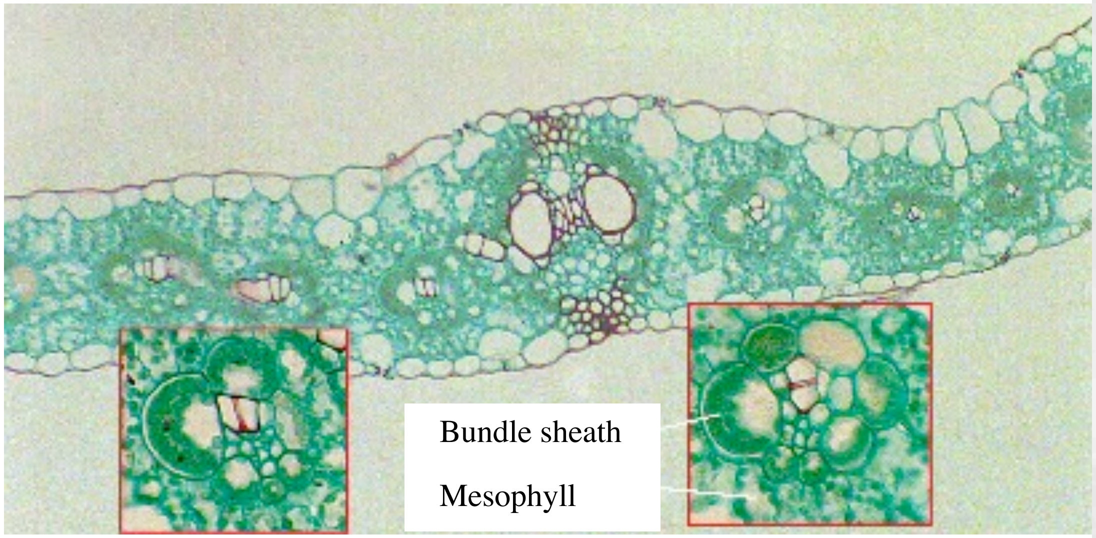
www.plantphys.net/ article.php?ch=e&id=290





Comparison of leaf anatomy of C3 and C4 plants. Reproduced through the courtesy of Dr. Stephen Grace, University of Arkansas.

Anatomy of C4 plants



Corn leaf cross-section

www.unlv.edu/.../ Anatomy/Leaves/Leaves.html

Kranz Anatomy
(Bundle Sheath Design)

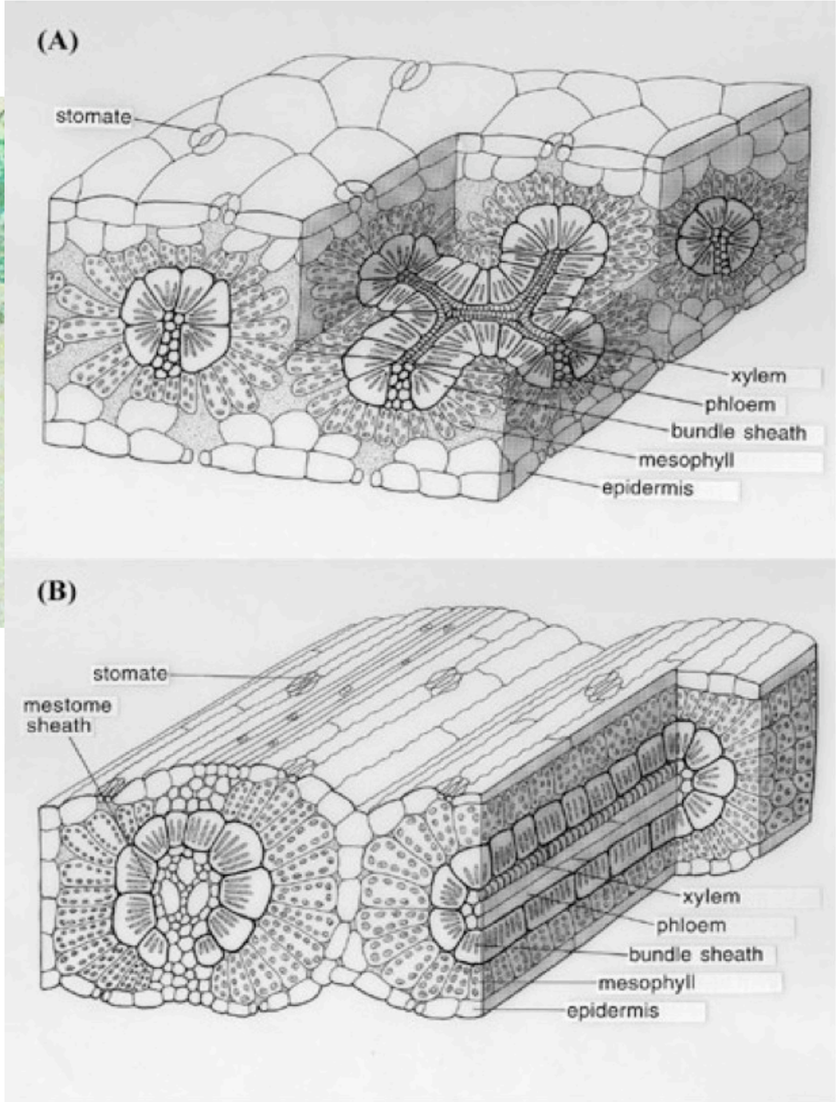


Figure 2 Diagrams of Kranz anatomy in a C4 dicot and a C4 grass. (A) In the C4 dicot *Atriplex rosea* (NAD-ME), the bundle sheath cells form only a partial sheath around the vascular tissue. Only the radially arranged mesophyll cells that are in contact with the bundle sheath express PEPCase. (B) In the C4 grass *Panicum capillare* (NAD-ME), the large vascular bundles are surrounded by both a non-photosynthetic bundle sheath (mestome sheath) and the photosynthetic bundle sheath.

www.plantphys.net/ article.php?ch=e&id=290

Central Steps in C4 photosynthesis

(1) Carboxylation of PEP (by PEP Carboxylase) produces C4 acids in the mesophyll cells

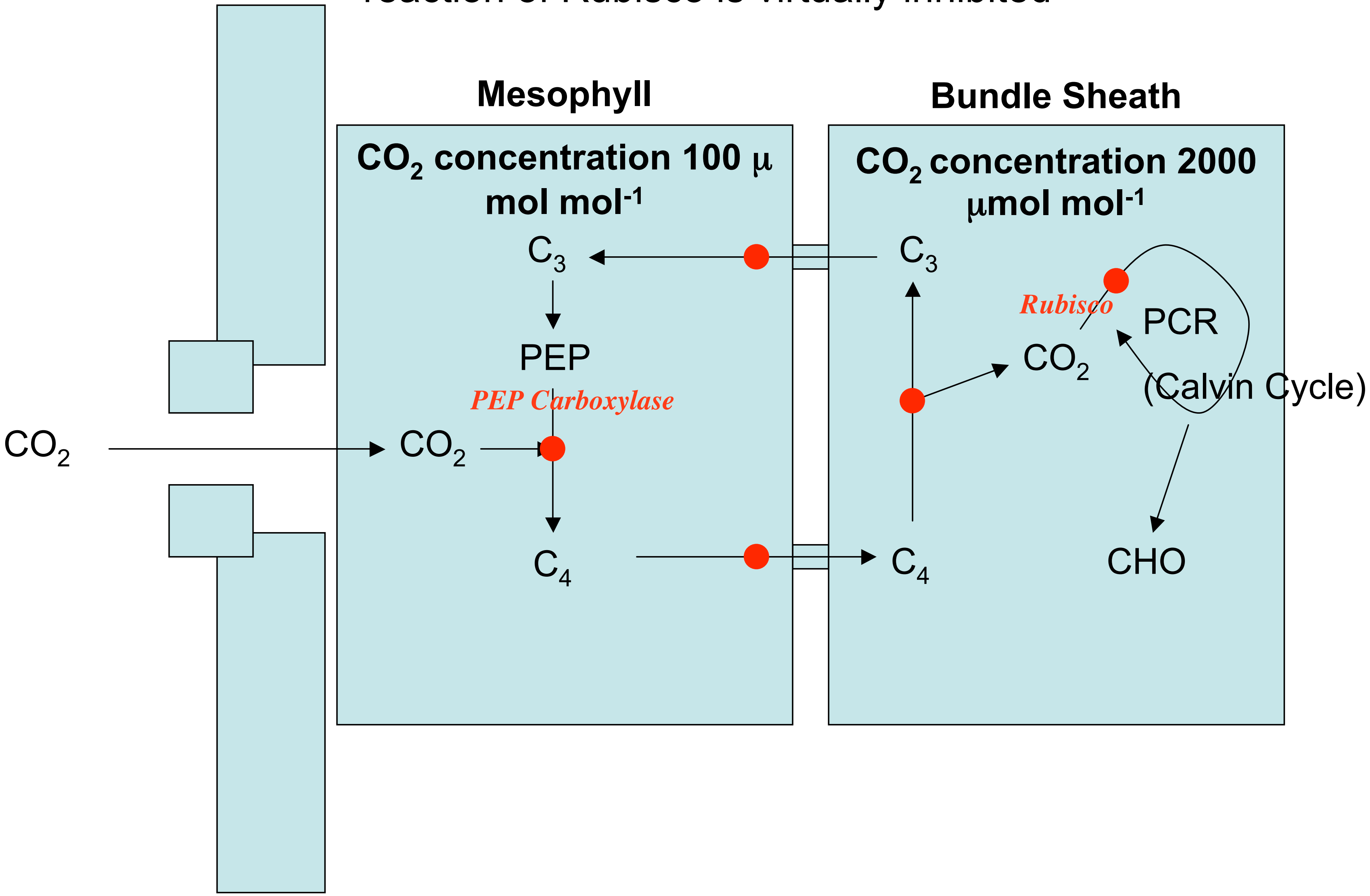
(2) Organic acids are transported to the bundle sheath cells

(3) Organic acids are decarboxylated in bundle sheath cells producing CO_2

(4) CO_2 is assimilated by Rubisco and PCR cycle

(5) Compounds return to the mesophyll cells to regenerate more PEP

C4 plants have a mechanism to enhance the partial pressure of CO_2 at the site of Rubisco - so that oxygenation reaction of Rubisco is virtually inhibited



Mesophyll

CO_2 concentration 100 μ mol mol^{-1}

Bundle Sheath

CO_2 concentration 2000 μmol mol^{-1}

Three subtypes of C4 photosynthesis (!)

Based on the enzyme involved in the decarboxylation of the C4 compounds transported to the vascular bundle sheath

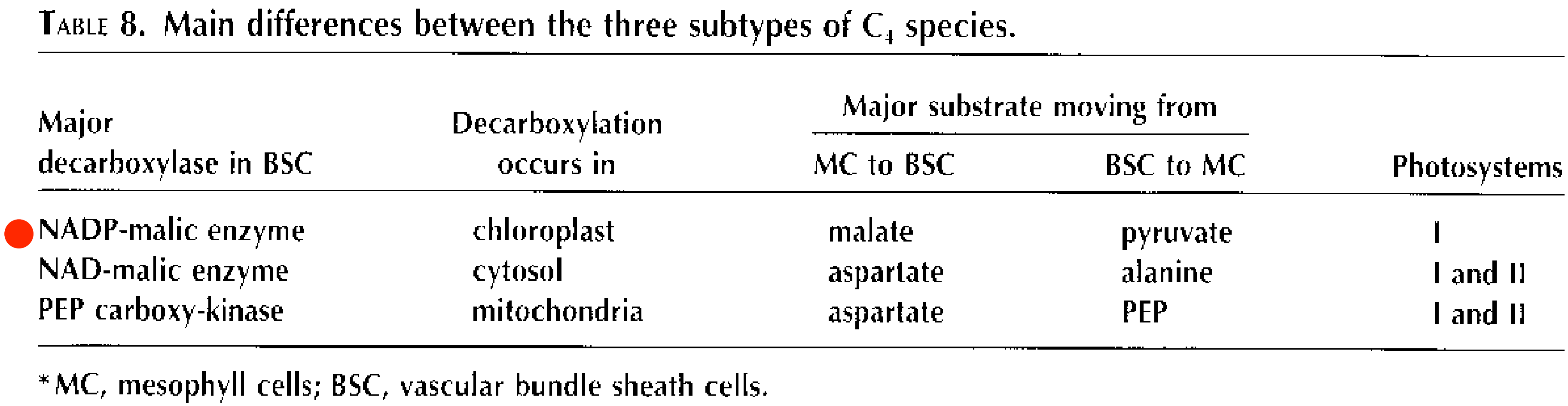
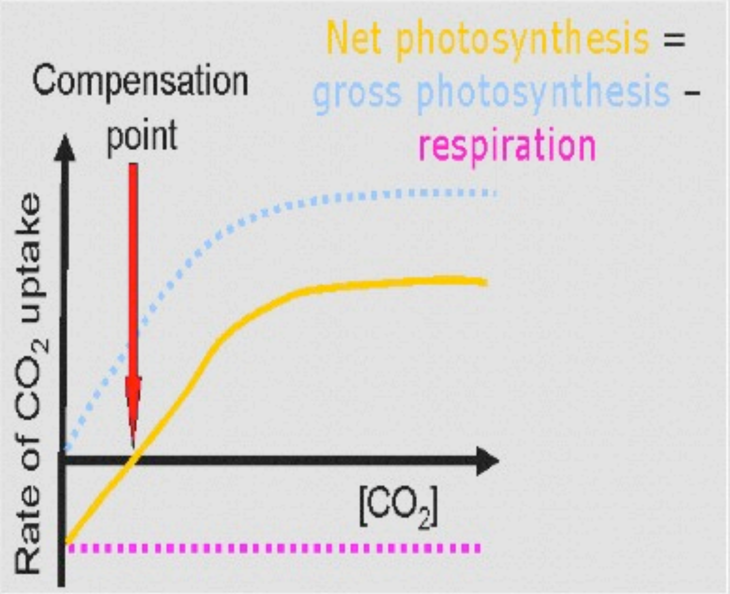


TABLE 8. Main differences between the three subtypes of C_4 species.

Major decarboxylase in BSC	Decarboxylation occurs in	Major substrate moving from MC to BSC	Major substrate moving from BSC to MC	Photosystems
● NADP-malic enzyme	chloroplast	malate	pyruvate	I
NAD-malic enzyme	cytosol	aspartate	alanine	I and II
PEP carboxy-kinase	mitochondria	aspartate	PEP	I and II

*MC, mesophyll cells; BSC, vascular bundle sheath cells.

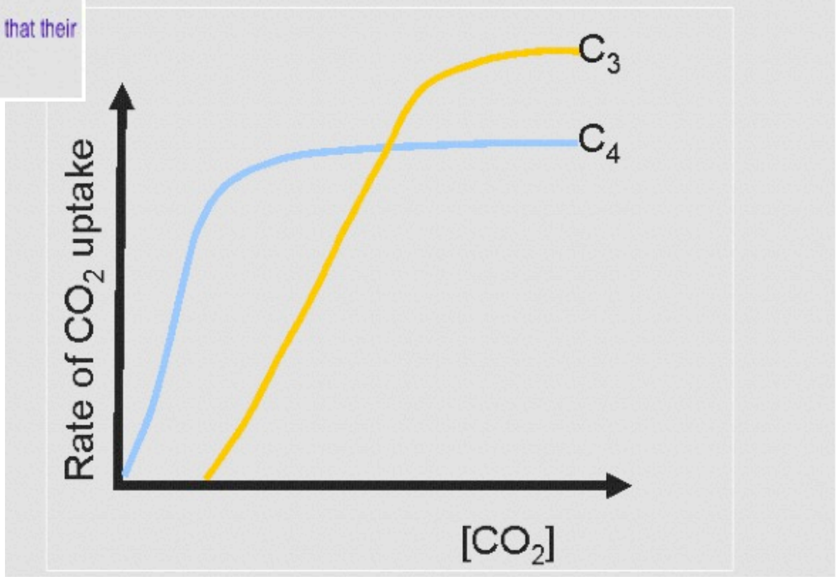
The Compensation Point



At the compensation point, photosynthesis is *just* too slow to outrun (mostly photo)respiration. C_3 plants photorespire so much, that their compensation point is *c.* 0.005%. C4 plants do not photorespire, so they have near zero compensation points.

Compensation points for C3 and C4 differ

Net Assimilation =
gross photosynthesis - respiration



http://www.steve.gb.com/science/photosynthesis_and_respiration.html

CAM

Generally in Succulent Plants

Cactaceae

Bromeliaceae

The first recognition of the nocturnal acidification process(CAM) can be traced to the Romans, who noted that certain succulent plants taste more bitter in the morning than in the evening.

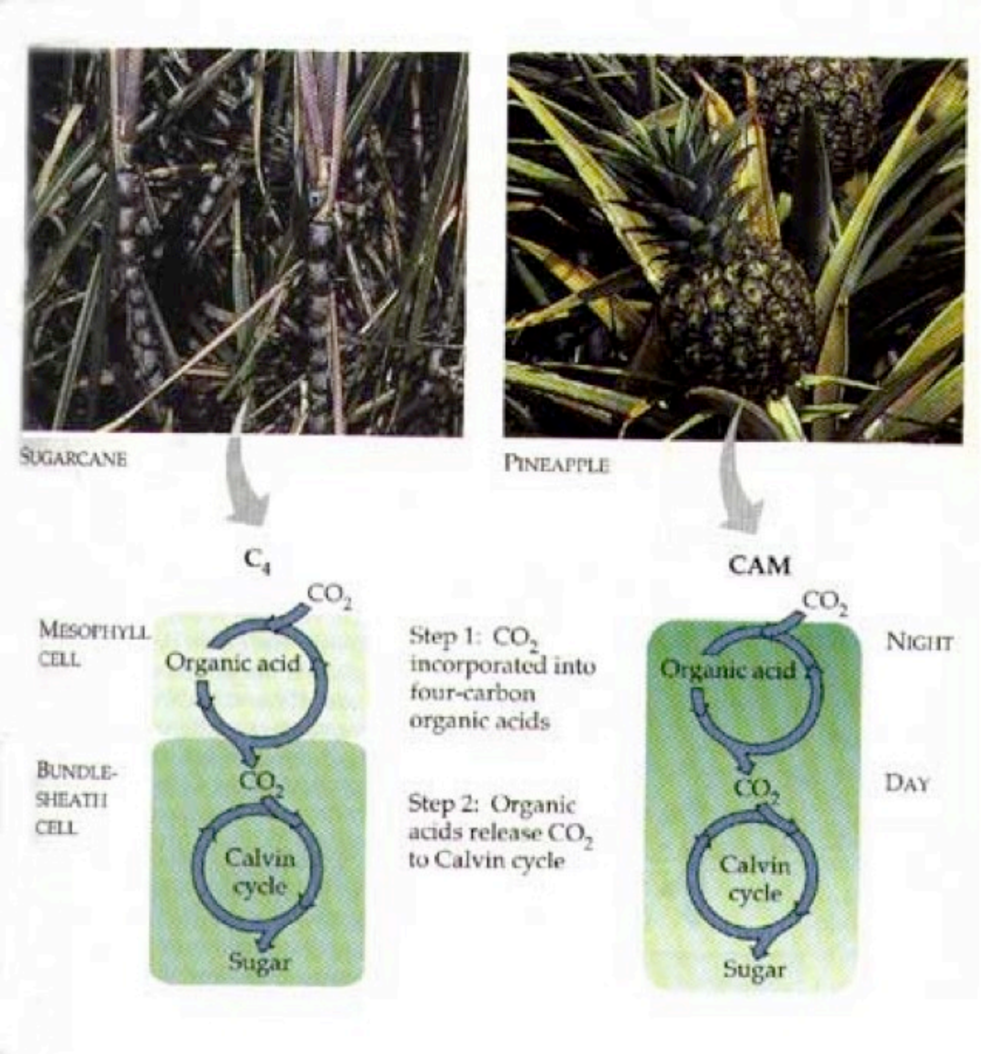
(Rowley, 1978)

CAM photosynthesis results in CO_2 concentration at the site of carboxylation

Comparing C4 and CAM photosynthesis

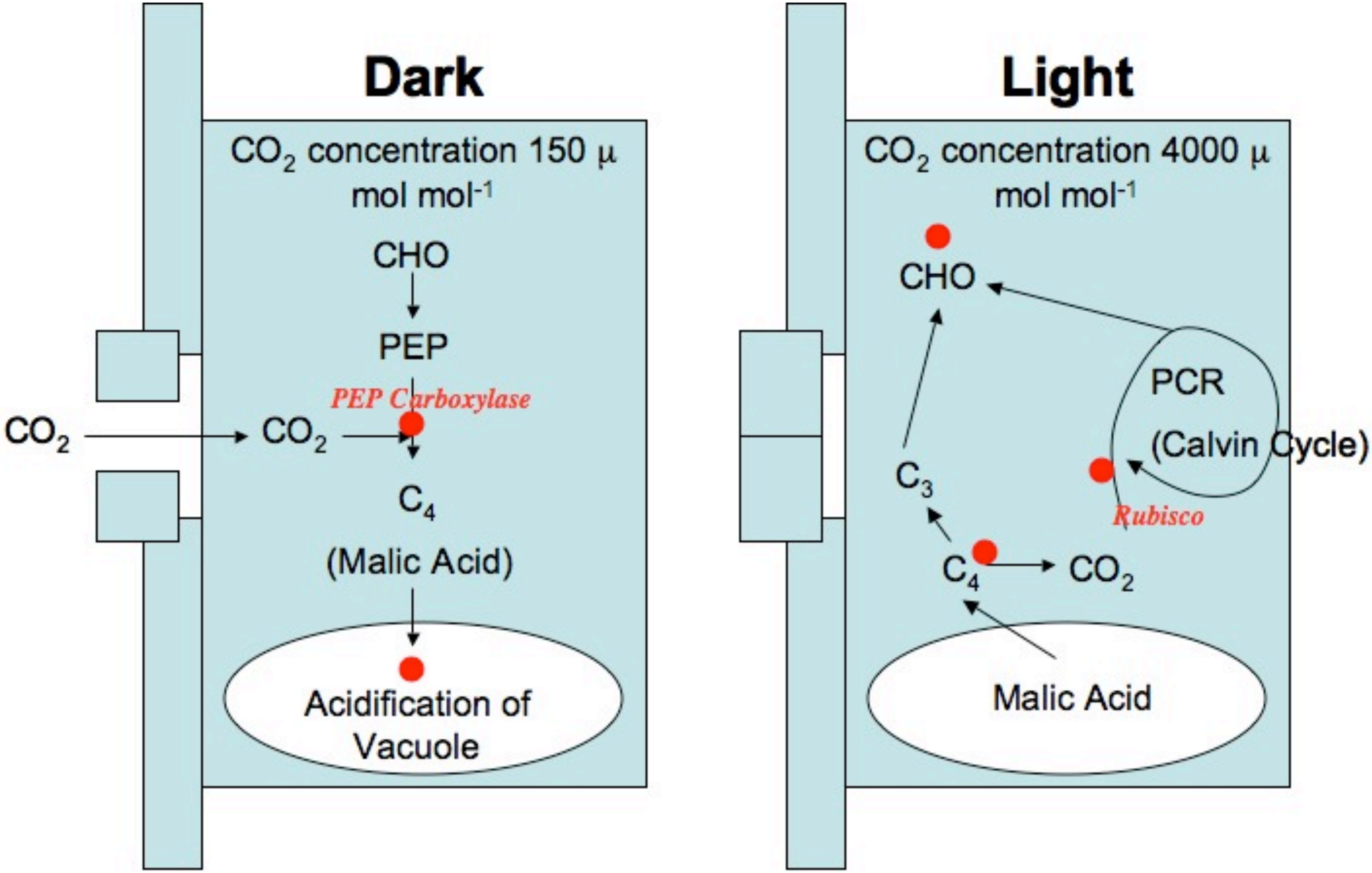
C4

CAM



The above diagram compares C4 and CAM photosynthesis. Both adaptations are characterized by initial fixation of CO_2 into an organic acid such as malate followed by transfer of the CO_2 to the Calvin cycle. In C4 plants, such as sugarcane, these two steps are separated spatially; the two steps take place in two cell types. In CAM plants, such as pineapple, the two steps are separated temporally (time); carbon fixation into malate occurs at night, and the Calvin cycle functions during the day. Both C4 and CAM are two evolutionary solutions to the problem of maintaining photosynthesis with stomata partially or completely closed on hot, dry days. However, it should be noted, that in all plants, the Calvin cycle is used to make sugar from carbon dioxide.

CAM PHOTOSYNTHESIS



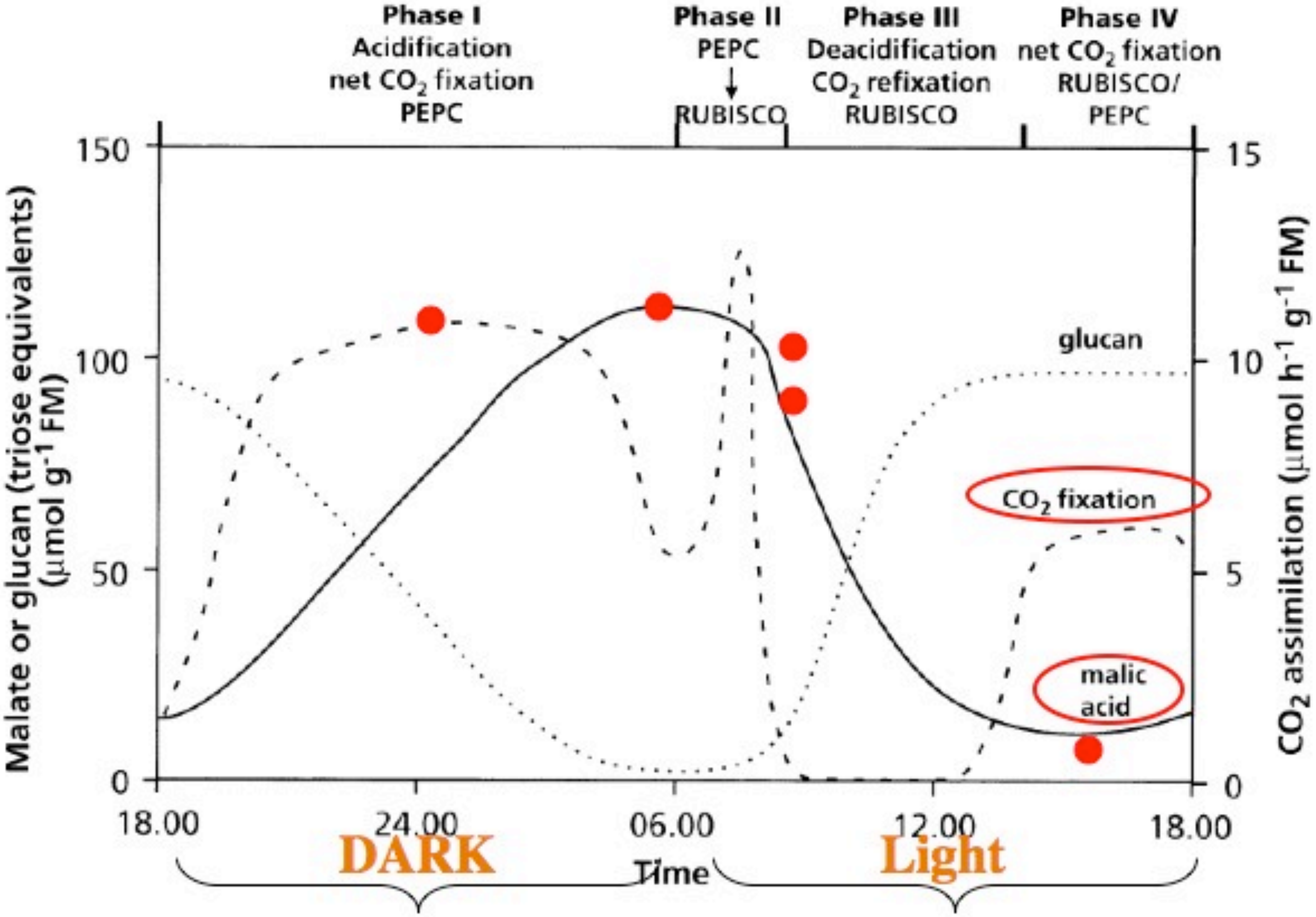


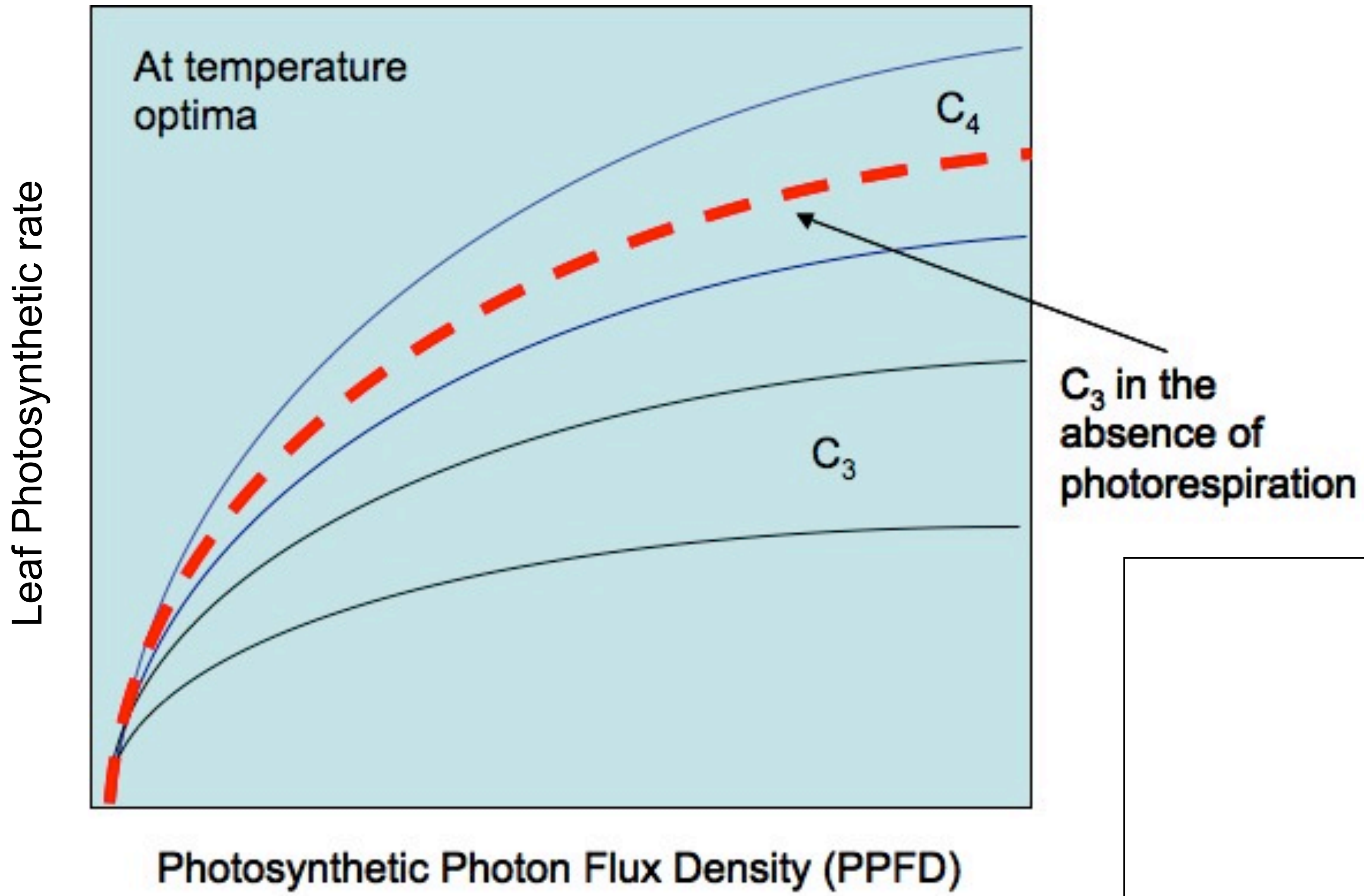
FIGURE 46. CO_2 fixation in CAM plants, showing diurnal patterns for stomatal conductance, net CO_2 assimilation, malic acid concentration, and carbohydrate concentrations; PEPC is PEP carboxylase (after Leegood & Osmond 1990, Osmond & Holtum 1981).

CO_2 Fixation = by *BOTH* PEP carboxylase and RUBISCO

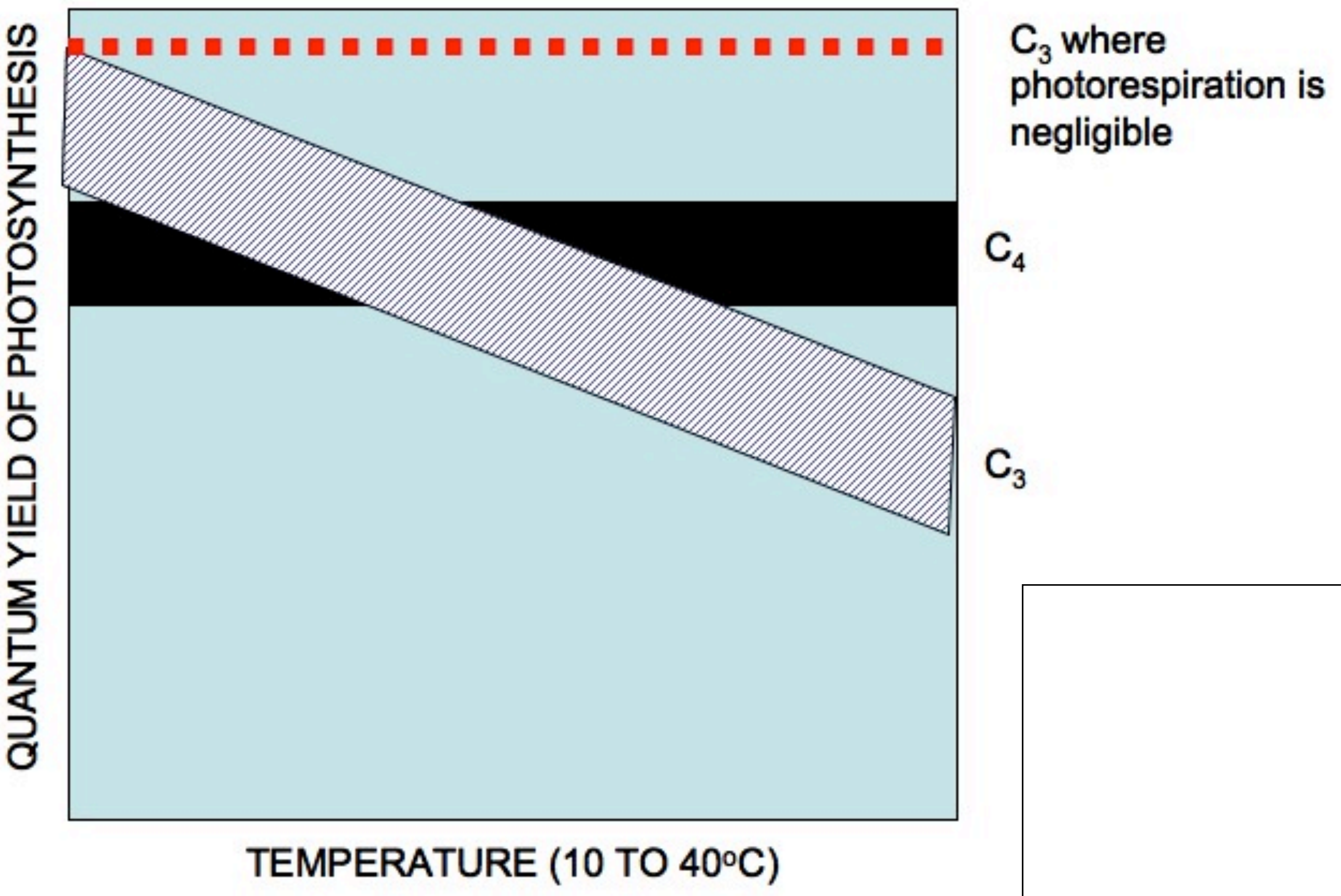
Functional consequences of C4 and CAM

- Light-use efficiency
- Water-use efficiency
- Nitrogen-use efficiency

Light-use efficiency



Light-use efficiency



Water-use efficiency

Recall

$$A/E = (C_a - C_i) / (1.6*Dw)$$

C4 and CAM photosynthesis change the **demand function** of photosynthetic activity (increase CO_2 flux)

Secondarily, reductions in E occur from

(1) Reductions in stomatal conductance
(2) Temporal dynamics of stomatal behavior

Consequences –

- C3 plants – 1 gram biomass per 650-800 grams water transpired
- C4 plants – 1 gram biomass per 250-350 grams water transpired
- CAM plants – 1 gram biomass per 100-200 grams water transpired

- **Rubisco in C3 plants represents up to 30%** of total leaf N (and sometimes up to 50%)

- C4 plants have **3 to 6 times less Rubisco** than C3 plants resulting in a **smaller N requirement** in leaves (120-180 mmol N m^{-2} and 200-260 mmol N m^{-2} respectively)

- CAM is more variable in N requirements and investments…but succulence is such a different morphological characteristic

Evolutionary Pressures leading to C4 and CAM

- Seems logical that selection for increased water-use efficiency and/or nitrogen-use efficiency would be the main selective pressures

C4 Photosynthesis has evolved independently many times . . .

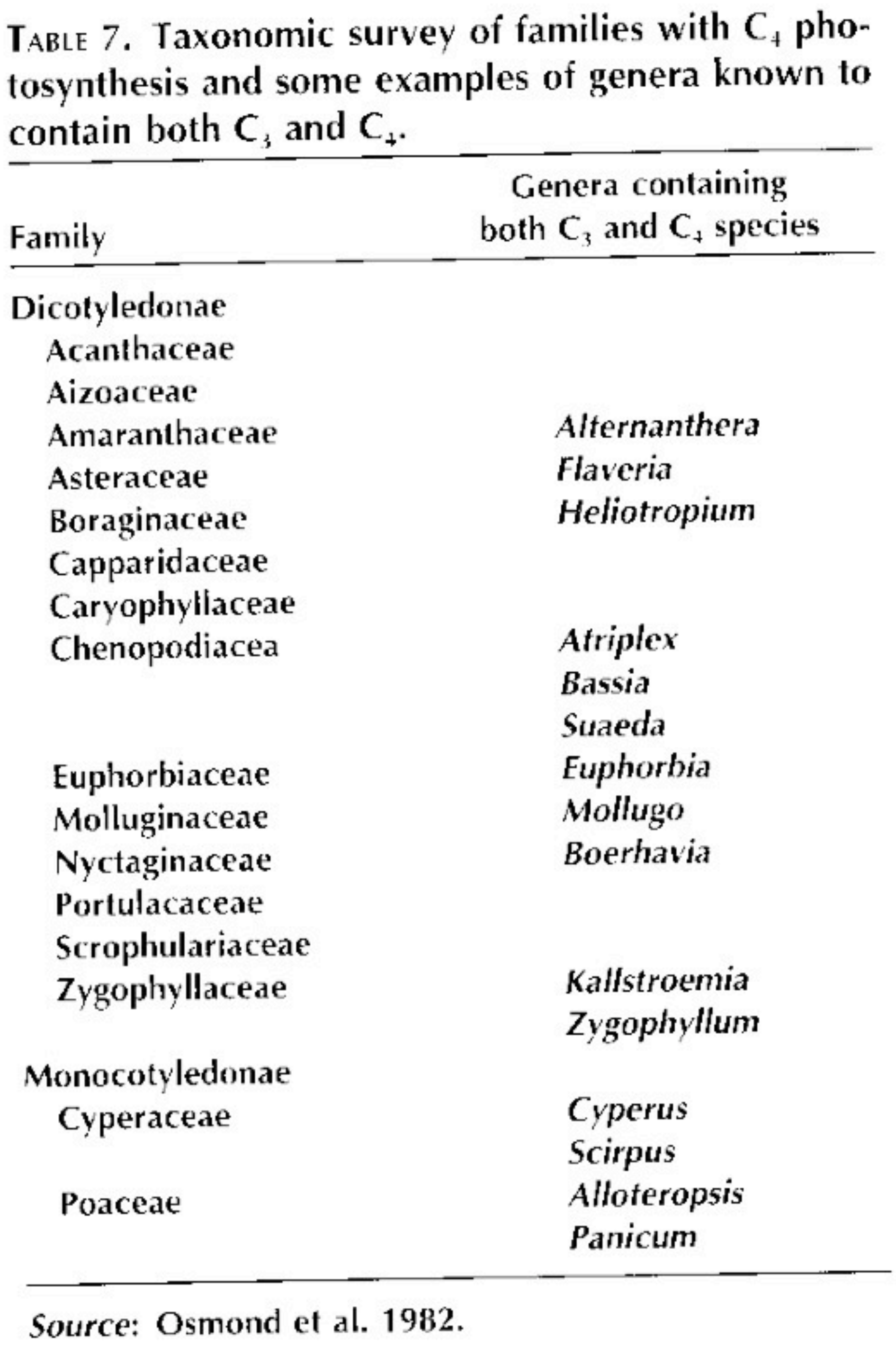


TABLE 7. Taxonomic survey of families with C_4 photosynthesis and some examples of genera known to contain both C_3 and C_4.

Family	Genera containing both C_3 and C_4 species
Dicotyledonae	
Acanthaceae	
Aizoaceae	
Amaranthaceae	*Alternanthera*
Asteraceae	*Flaveria*
Boraginaceae	*Heliotropium*
Capparidaceae	
Caryophyllaceae	
Chenopodiacea	*Atriplex* *Bassia* *Suaeda*
Euphorbiaceae	*Euphorbia*
Molluginaceae	*Mollugo*
Nyctaginaceae	*Boerhavia*
Portulacaceae	
Scrophulariaceae	
Zygophyllaceae	*Kallstroemia* *Zygophyllum*
Monocotyledonae	
Cyperaceae	*Cyperus* *Scirpus*
Poaceae	*Alloteropsis* *Panicum*

Source: Osmond et al. 1982.

Evolution of the C4 Syndrome is a recent event in the history of plants

- First evolved 12.5 million years ago

-Only found within the Angiosperms

- mainly in the monocots but also within several Eudicot families
- not found in trees

Evolution of C3 - Atmospheric [CO_2] was much greater

But with the success of plants [CO_2] decreased and [O_2] increased

-> *conditions that increase photorespiration*

-> *Favoring adaptations that increase CO_2 concentrating adaptations*

Factors favoring C4 evolution

-
  - Starting around 40 million years ago
  - Increased photorespiration in C3 plants
- Secondarily
  - Higher day temperatures
  - Limited water

Water use efficiency is regarded as main selective trait favoring evolution of C4 over C3 photosynthesis in hot, dry conditions (with low [CO_2] relative to [O_2])

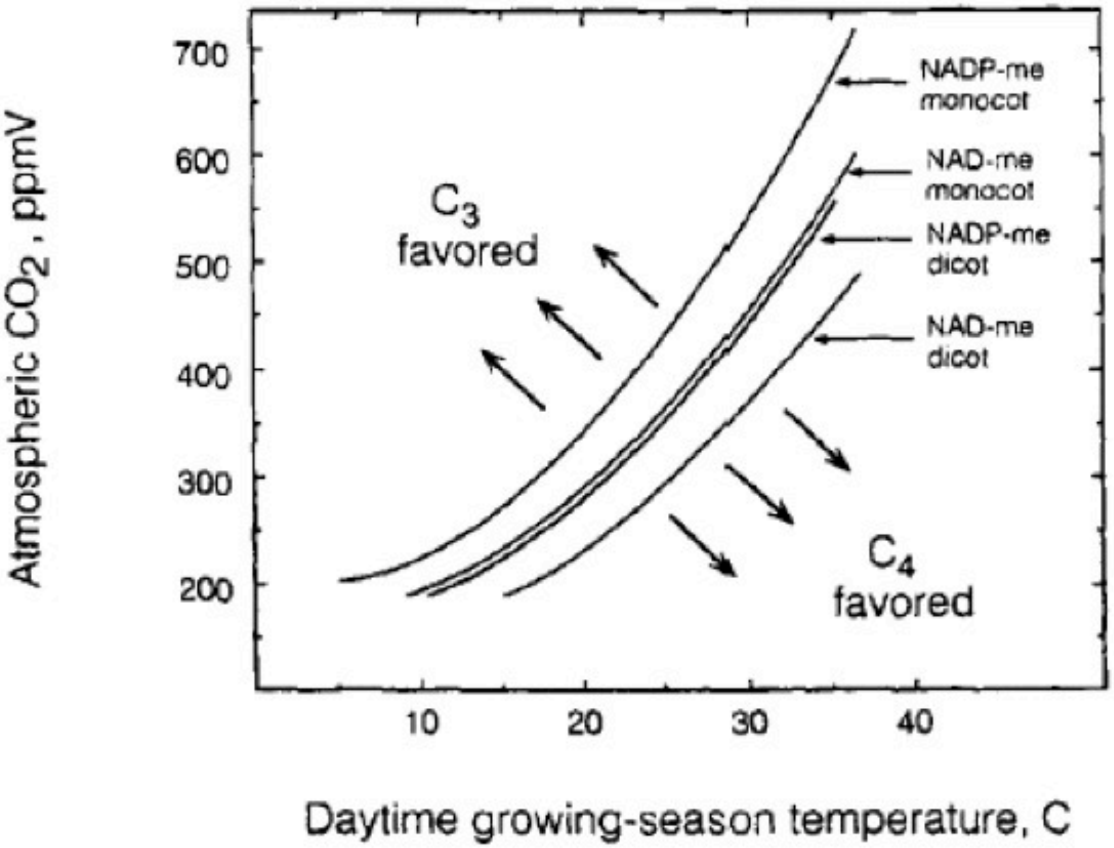


Fig. 6 Modeled crossover temperatures of the quantum yield (defined as the leaf level ratio of photosynthetic carbon gain to photons absorbed) as a function of atmospheric CO_2 concentrations and daytime growing season temperature under saturating light conditions. Boundary conditions vary between monocots and dicots and between different decarboxylase subtypes and are defined as the temperature at which a particular CO_2 results in quantum yields for CO_2 uptake that are equivalent between C_3 and C_4 species (from Ehleringer et al. 1997; reprinted with permission of Springer).

Other hypotheses

- C4 plants are less nutritious than C3 plants (less N,P, CHO per gram leaf)
- C4 herbivores seem to be ‘specialized’
- Could a C4 syndrome be an escape from herbivory?

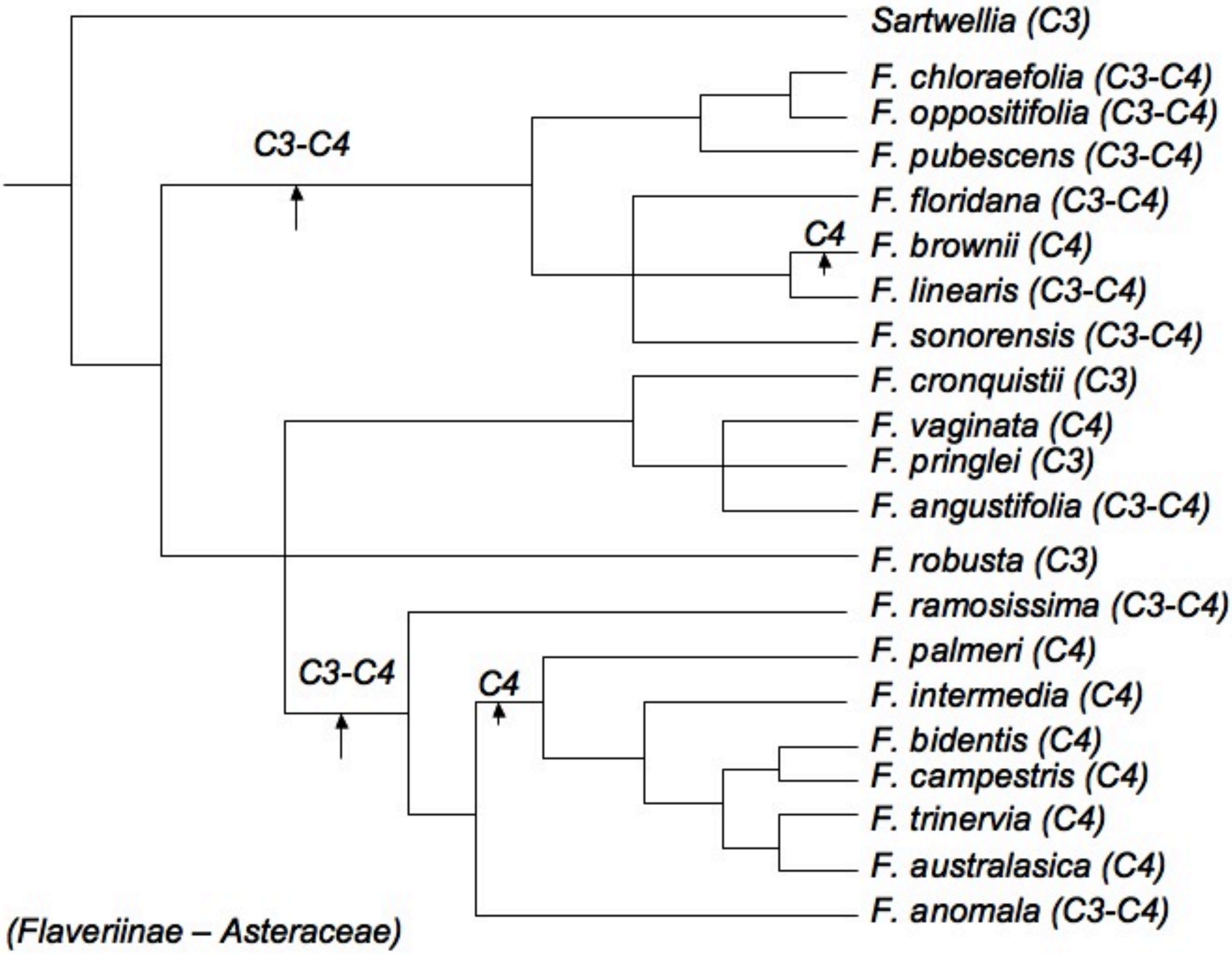
C3-C4 intermediates

- In several groups, there are biochemical and morphological intermediates
- Represent and evolutionary transition?
- Useful tool in understanding performance of transition states

Intermediates appear to have evolved multiple times

- Found in 6 families across Monocots and Eudicots

Flaveria linearis


Sartwellia (C3)
F. chloraefolia (C3-C4)
F. oppositifolia (C3-C4)
F. pubescens (C3-C4)
F. floridana (C3-C4)
F. brownii (C4)
F. linearis (C3-C4)
F. sonorensis (C3-C4)
F. cronquistii (C3)
F. vaginata (C4)
F. pringlei (C3)
F. angustifolia (C3-C4)
F. robusta (C3)
F. ramosissima (C3-C4)
F. palmeri (C4)
F. intermedia (C4)
F. bidentis (C4)
F. campestris (C4)
F. trinervia (C4)
F. australasica (C4)
F. anomala (C3-C4)
C3-C4
C4
C3-C4
C4
(Flaveriinae – Asteraceae)

CAM Evolution

- Evolved from C3 plants BEFORE evolution of C4 plants - since middle Tertiary 20-30mya (aquatic species)

- Found in 2x as many families than C4

- Phylogenetically diverse

  Lycophyte, Pterophyta, Gnetophyta, **Angiosperms**

-Selection favoring maximizing carbon assimilation

-Selection to overcome CO_2 limitations during the day

- 6% of terrestrial and aquatic flora is CAM

- Unlike C4

Examples of CAM plants at very high elevations 4700m (!)

- Usually associated with succulence

Cactus, Iceplant, Stonecrop, Euphorbs
Bromeliads, Orchids

Many tropical forest epiphytes

- CAM is also found in aquatic vascular plants where it presumably enhances inorganic carbon acquisition in certain aquatic environments where CO_2 availability can become rate limiting for photosynthesis

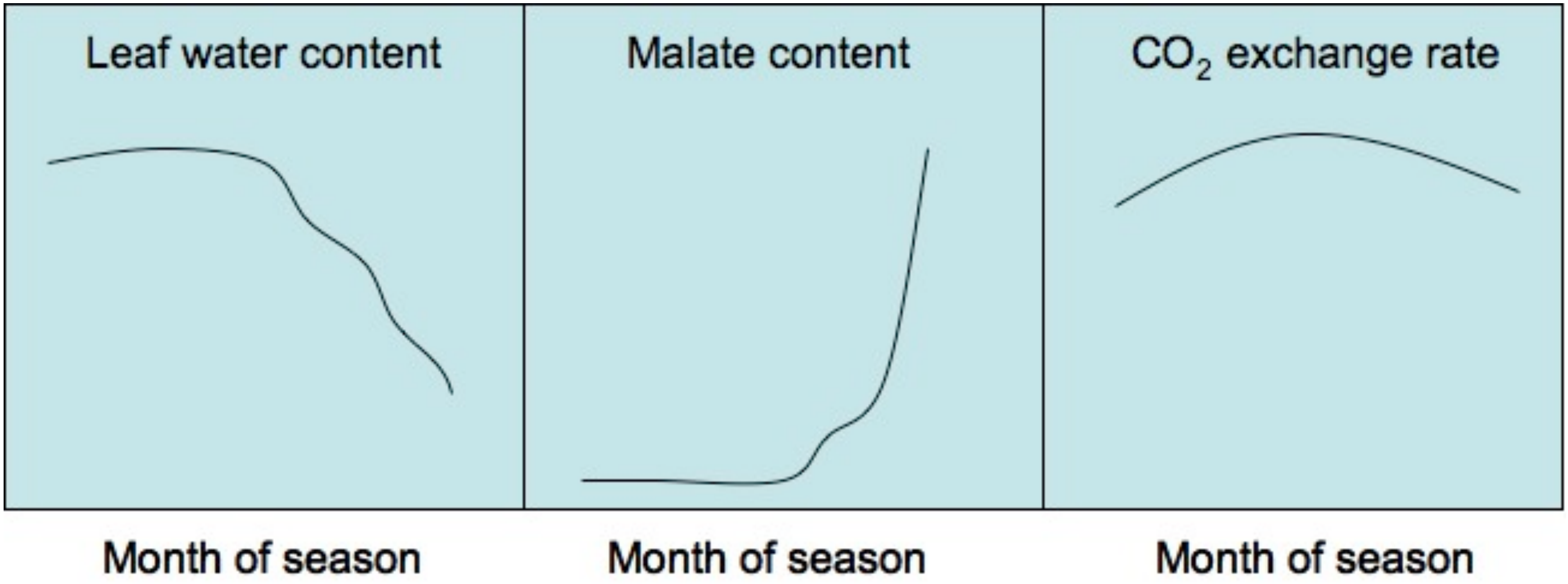
-Presence of CAM declines when night time temps are high

Variable photosynthetic strategies

Iceplant (Aizoaceae)

Mesembryanthemum sp.

- *Mesembryanthemum crystallinum*
  - C3 during high leaf water content but induction of CAM during drying
  - Result - Maintenance of photosynthetic rate throughout the year



Vernal Pools: Example of diversity of photosynthetic strategies

http://www.vernalpools.org/

http://ceres.ca.gov/wetlands/whats_new/vernal_sjq.html

Jon Keeley – California Vernal Pools

ISOETACEAE
Lycophyta

BRAXENGRÄS, ISOËTES LACUSTRIS L.

- Quillwort – *Isoetes howelii* – CAM, but switches to C3 when not submerged
- Quillworts – *I. howelii & I. orcuttii* – use channels in roots to enhance CO_2 uptake (from submegred soils)
- Aquatic grass – *Orcuttia californica* – uses C4, with submerged and aerial leaves
- Aquatic plant – *Eleocharis acicularis* – Grass, uses C4 when submerged, shifts to C3 when exposed to the atmosphere

All in a very localized plant community!
Strategies likely evolved independently

Photosynthetic Distributions

- Associated with changes in selective pressures on water-use and nutrient use efficiency

C₄ Plants 71

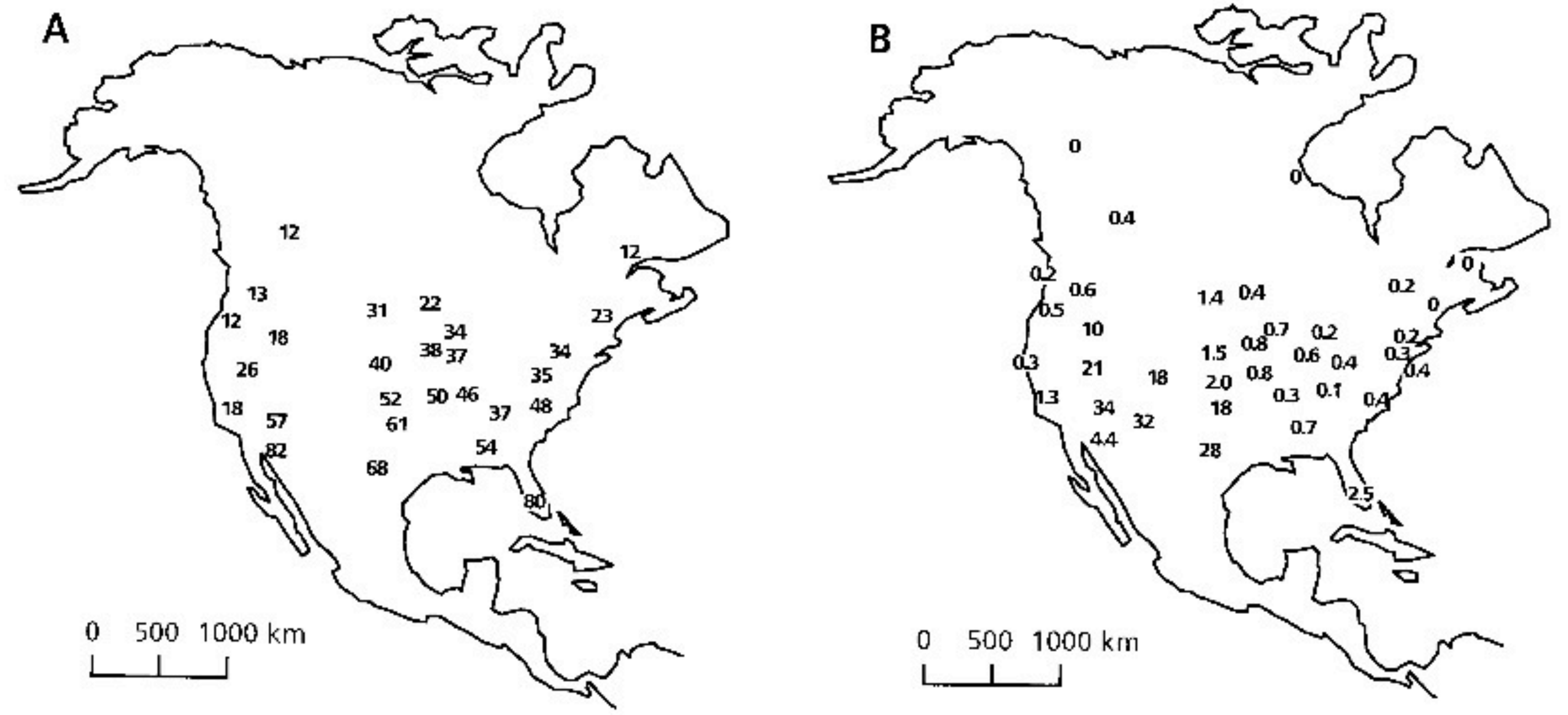


FIGURE 42. Geographic distribution of C_4 species in North America. (A) percentage of grass taxa that are C_4 plants. (B) percentage of dicotyledon taxa that are C_4 plants in regional floras of North America (Teeri & Stowe 1976, and Stowe & Teeri 1978, as cited in Osmond et al. 1982).

C4 species are more dominant in hot, dry, nitrogen limiting environments

TABLE 1. Rough estimates of the number of grass species worldwide that use each biochemical variant of C_4 photosynthesis. Genera that have not yet been biochemically typed are assumed to have the same proportions of the different C_4 variants as the genera within their tribe that have been biochemically typed. In genera in which there is known variation for C_4 pathway, it is assumed that the proportion of species using each variant is the same among species not yet biochemically typed as among species that have been. This table does not include C_3 species, which are also found in each subfamily. Information was compiled from Willis and Airy Shaw (1966), Brown (1977), Hattersley (1987), Hattersley and Watson (1992), Sage, Li, and Monson (1999), and Watson and Dallwitz (1999).

Grass subfamily	NADP-ME	NAD-ME	PCK
Arundinoideae	372	4	0
Chloridoideae	9	957	431
Panicoideae	2476	250	167

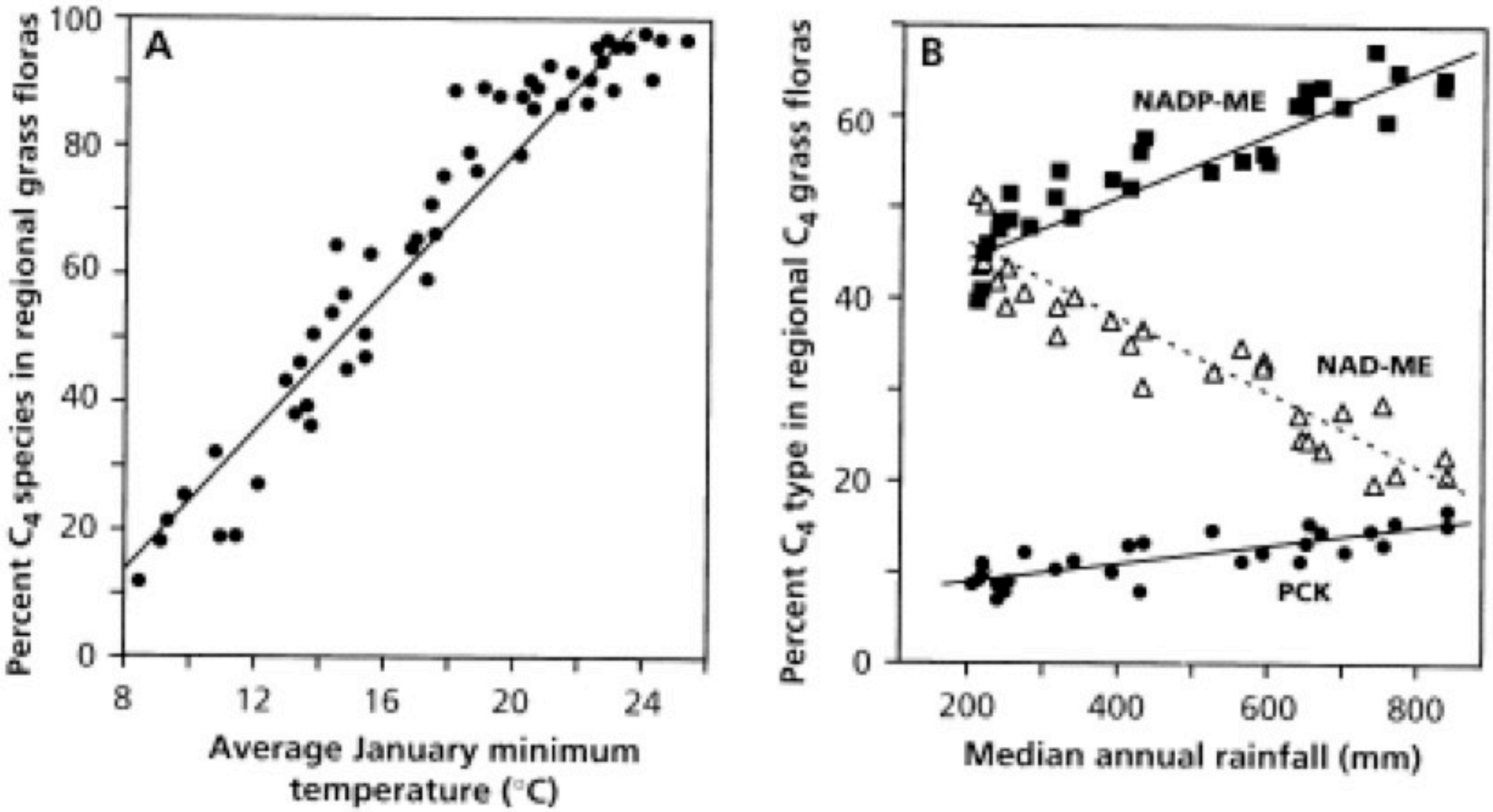


FIGURE 43. (A) The percentage occurrence of C_4 metabolism in grass floras of Australia in relation to temperature in the growing season (January). (B) The percentage occurrence of C_4 grass species of the three metabolic types in regional floras in Australia in relation to median annual rainfall (Henderson et al. 1995).

Questions

-What is PEP carboxylase?

-Outline the similarities between C3, C4, and CAM photosynthesis

-Outline the differences between C3, C4, and CAM photosynthesis

-What selective pressures lead to C4 and CAM pathways?

-Why aren’t all plants C4 or CAM?