ECOFISIOLOGIA VEGETAL

BT 791 Tópicos de Ecologia Vegetal

2º Semestre de 2017

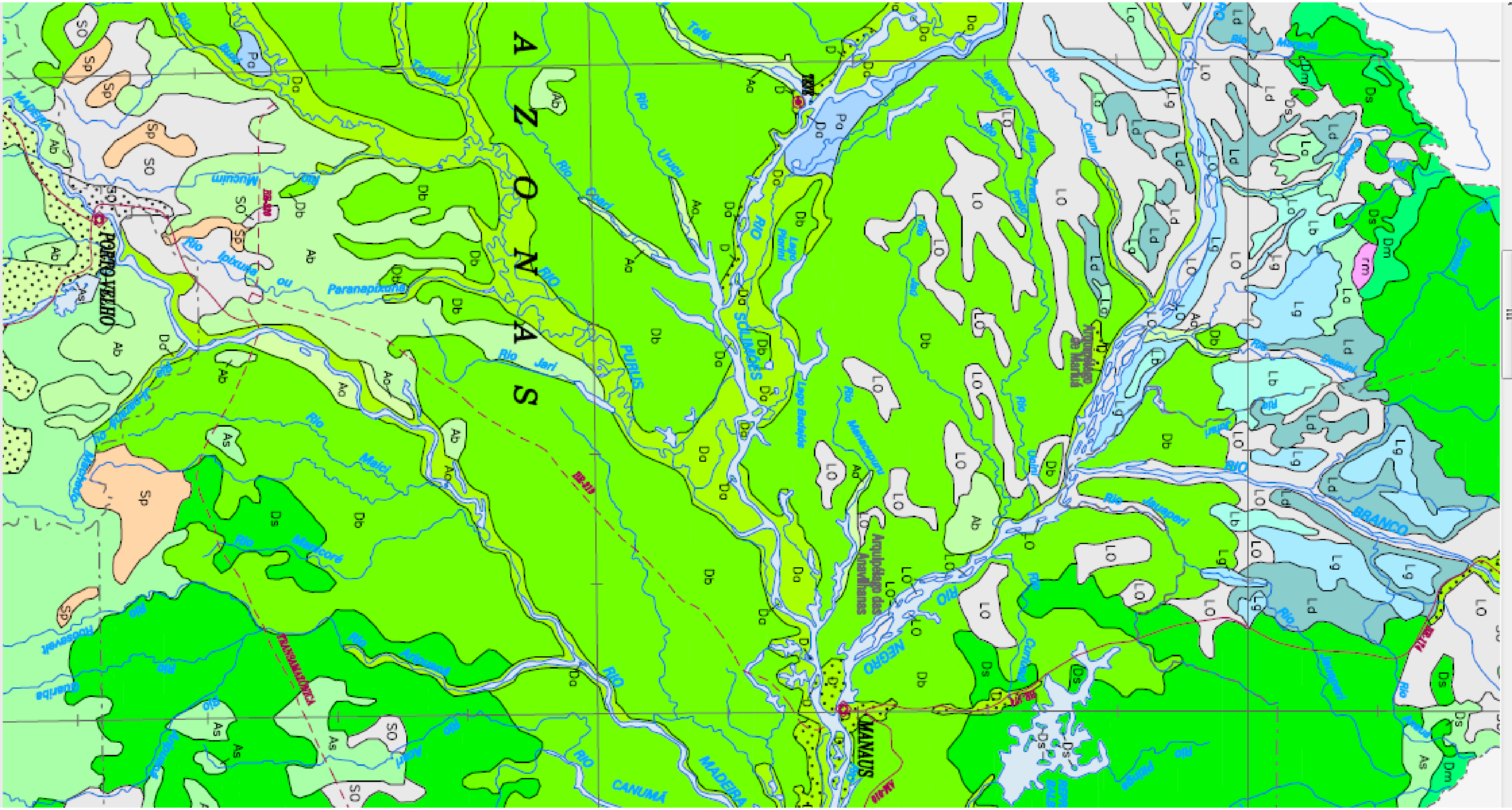
01/09/2017

Carlos A. Joly

Até recentemente a florada dos ipês estava relacionada ao número de horas entre o excesso de Vermelho Extremo do Nascer do Sol e o Excesso do Vermelho Extremo do Por do Sol. Mediada, portanto, pelo **fitocromo.**

Nos últimos anos comprovou-se que este é mais um fenômeno que responde a diversos fatores simultaneamente: duração de horas do dia (ou da noite), disponibilidade hídrica, alternância de temperatura e, talvez outros que ainda desconhecemos.


BIOMA AMAZÔNIA
BIOMA CAATINGA
BIOMA CERRADO
BIOMA PANTANAL
BIOMA MATA ATLÂNTICA
BIOMA PAMPA



FLORESTAS DE VÁRZEA & FLORESTAS IGAPÓ (rios de águas escuras – por exemplo o Rio Negro) – sazonalmente inundadas


Parque Nacional de Anavilhanas Rio Negro


Mata de Igapó – Arquipélago de Anavilhanas Rio Negro

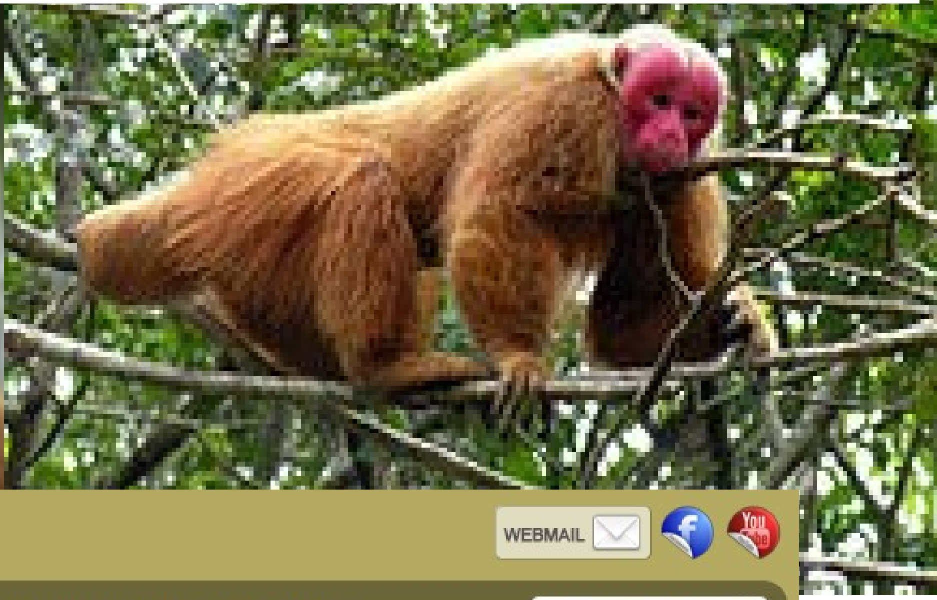
Ingá – *Inga* spp (Fabaceae - Mimosoideae

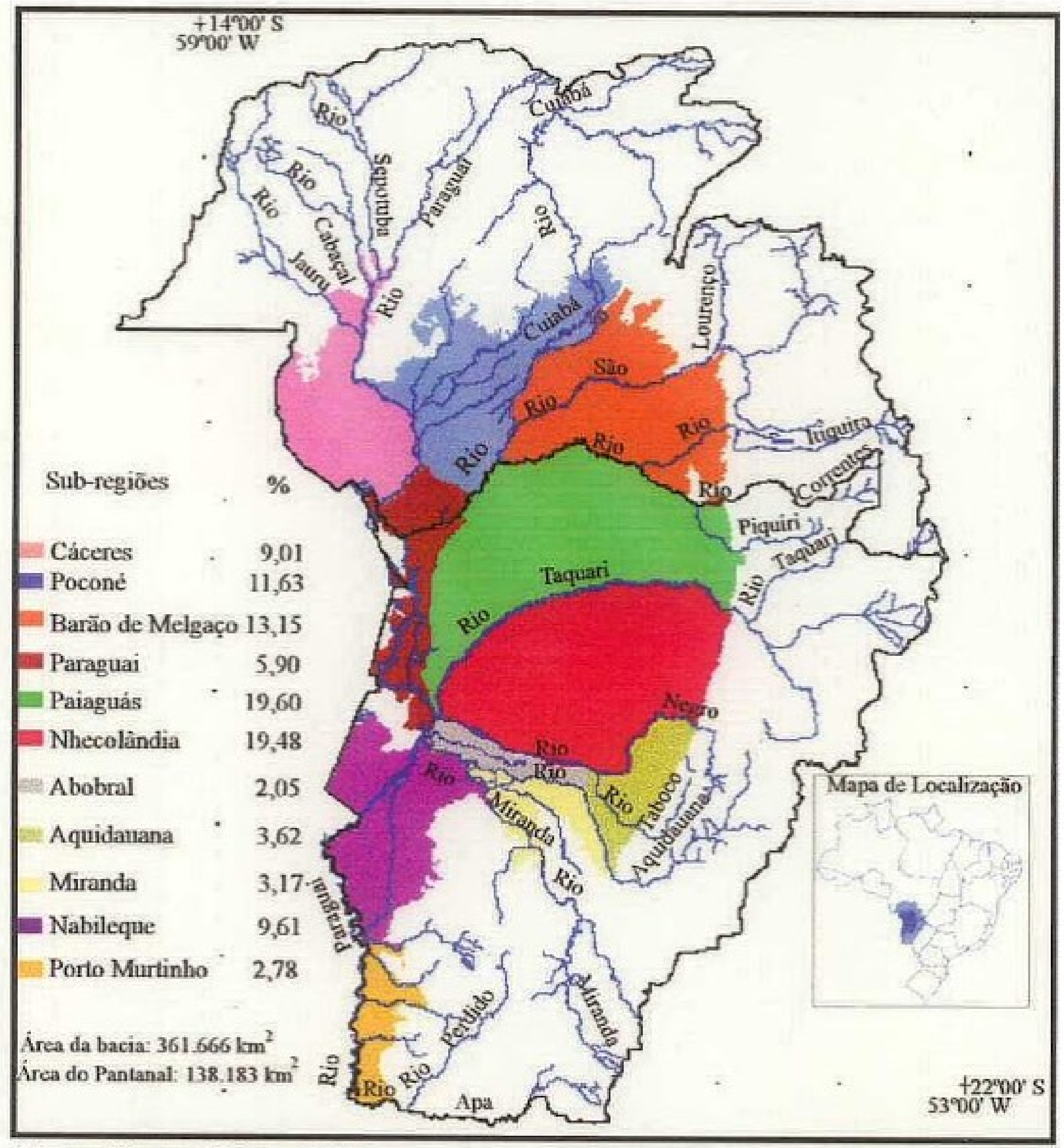
Munguba - *Pachira* spp (Bombacaceae)

Seringueira *Hevea brasiliensis L.*(Euphorbiaceae)

Tambaqui (*Colossoma macropomum* Cuvier, 1818)

Uacari (*Cacajao calvus* ssp)





Fonte: Silva e Abdon, 1998

Vista aérea do Pantanal da Nhecolandia/MS

THE FLOOD PULSE CONCEPT – teoria proposta em 1989 por Junk e colaboradores para as áreas inundáveis da Amazônia revista e ampliada em 2004 para incluir o Pantanal.

Junk W.J & Wantzen K.M. 2004 THE FLOOD PULSE CONCEPT: NEW ASPECTS, APPROACHES AND APPLICATIONS - AN UPDATE. In Welcomme, R. & Toledo, P. (eds) Proceedings of the second international symposium on the management of large rivers for fisheries. FAO, 117-149.

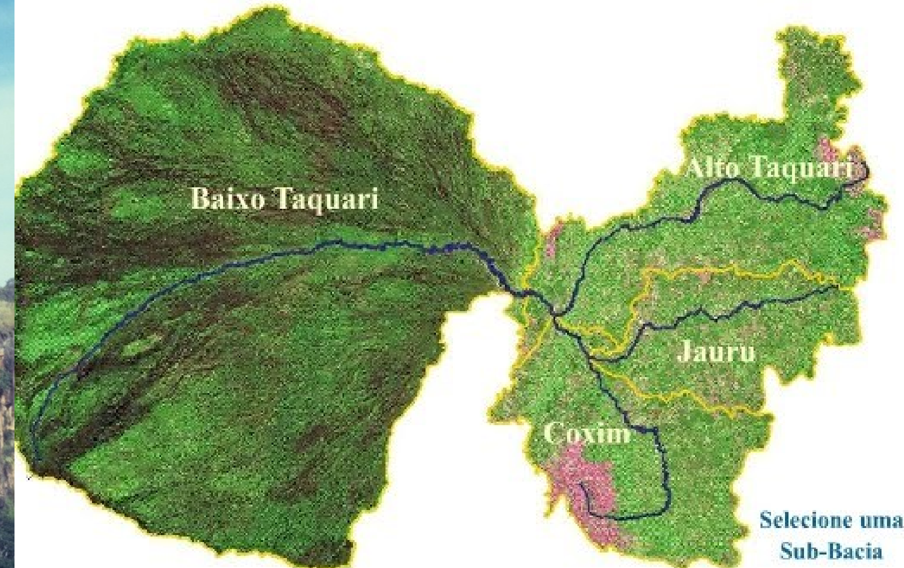


Foto: João Vila

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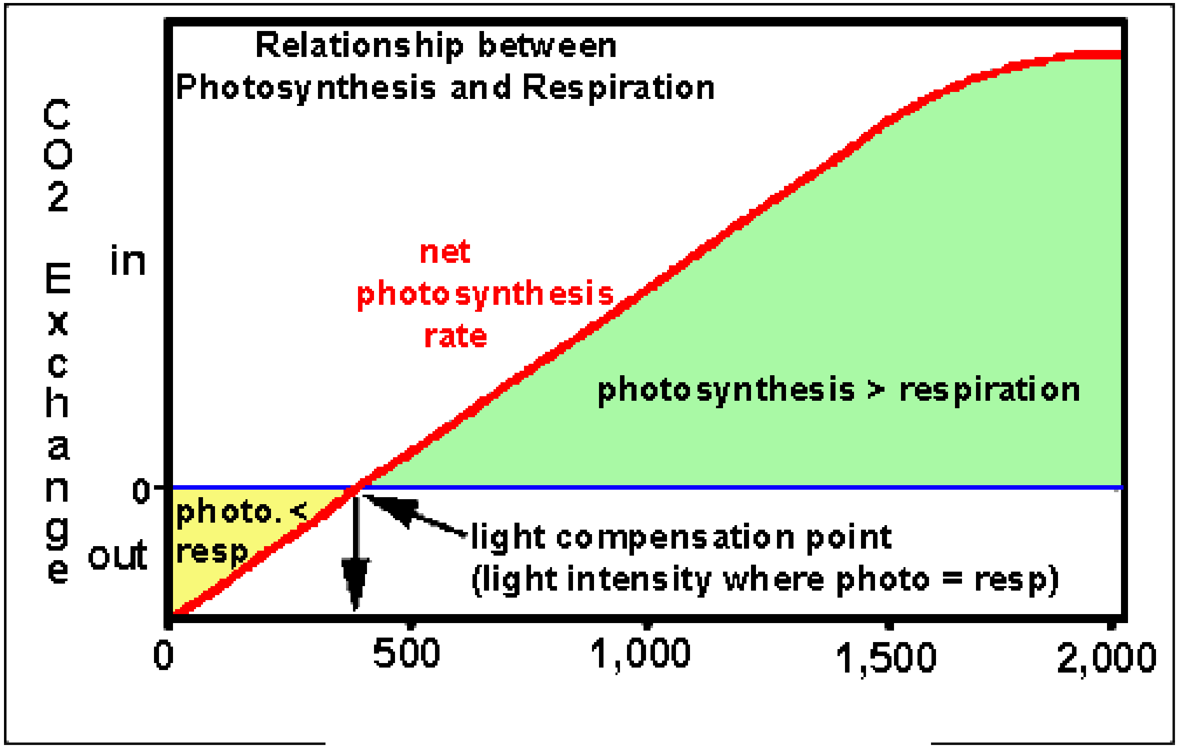
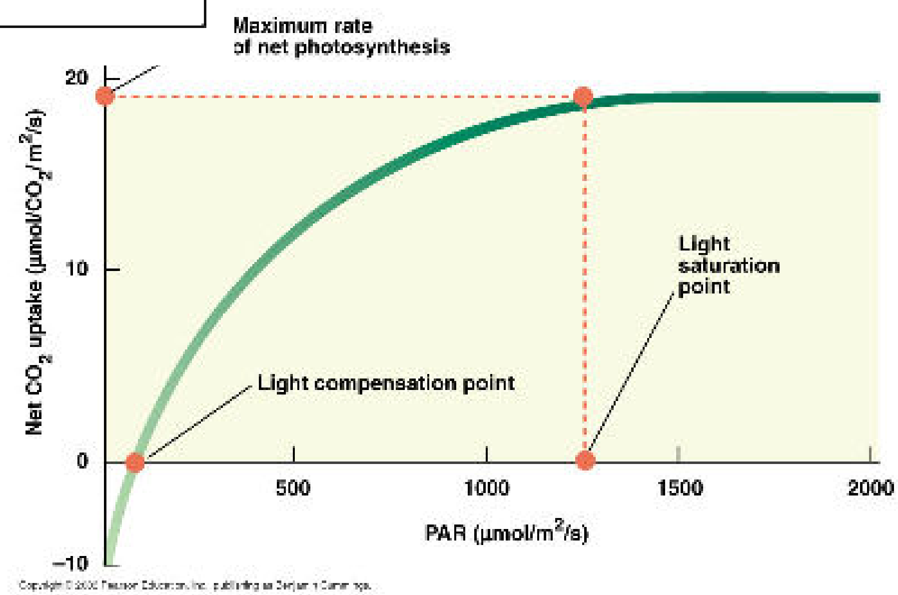


Relationship between
Photosynthesis and Respiration
CO2 Exchange
in
out
0
net
photosynthesis
rate
photosynthesis > respiration
photo. <
resp
light compensation point
(light intensity where photo = resp)
0
500
1,000
1,500
2,000



Maximum rate
of net photosynthesis
Net CO2 uptake (μmol/CO2/m2/s)
20
10
0
−10
Light compensation point
Light
saturation
point
500
1000
1500
2000
PAR (μmol/m2/s)

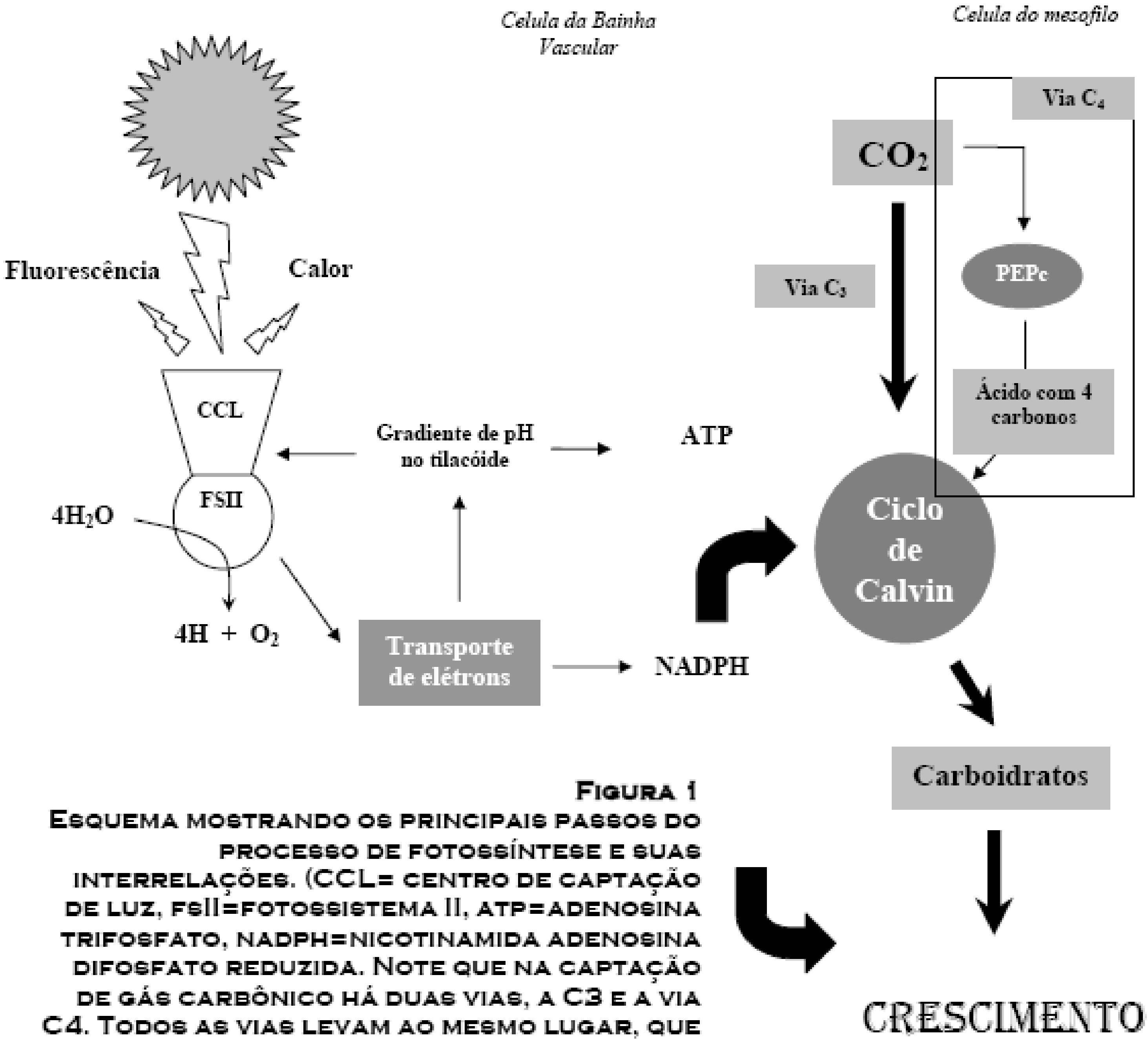


Figura 1

Esquema mostrando os principais passos do processo de fotossíntese e suas interrelações. (CCL= centro de captação de luz, FSII=fotossistema II, ATP=adenosina trifosfato, NADPH=nicotinamida adenosina difosfato reduzida. Note que na captação de gás carbônico há duas vias, a C3 e a via C4. Todos as vias levam ao mesmo lugar, que é produzir carboidratos que serão

It has been estimated that 200 Billion tons of Carbon is fixed as Carbohydrates each year. Marine Plankton accounts for 40% of this.

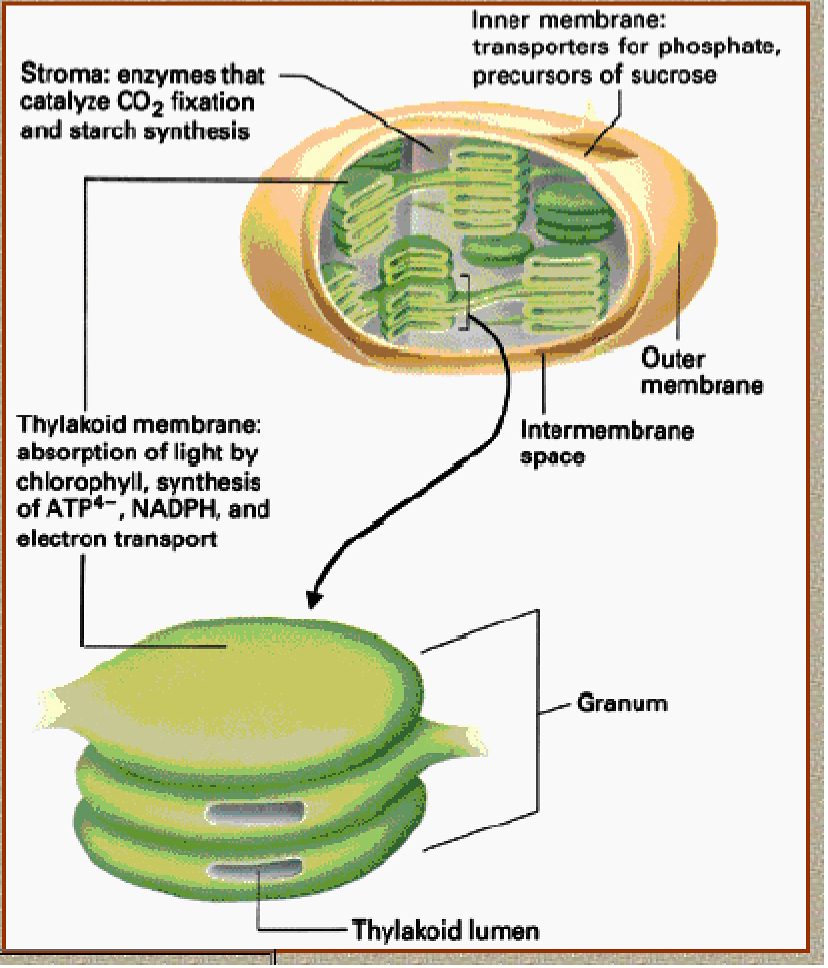
The biochemical steps for this occur in the Chloroplast Stroma. Consequently, these can be called Stroma Reactions.

Melvin Calvin elucidated the basic steps in this process and they are often referred to as the Calvin Cycle.

The first product of CO_2 fixation is a 3-Carbon unit. Consequently, this can be called C3 Photosynthesis.

There are three basic events which characterize this process.

They are Carboxylation, Reduction & Regeneration.

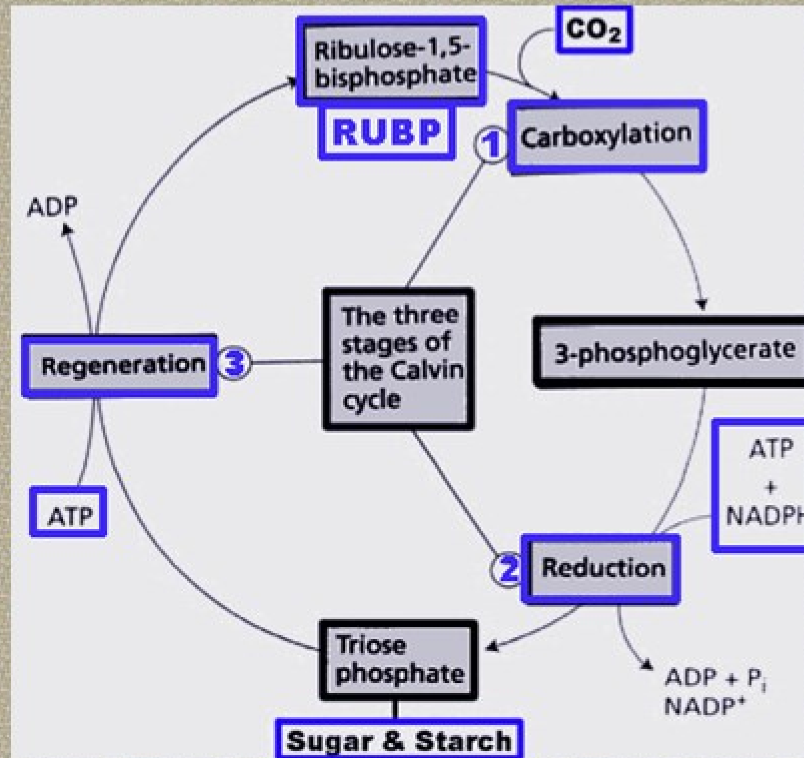


The first step involves the addition of CO_2 to a 5-Carbon acceptor [RUBP].

This leads to the production of two 3-Carbon molecules.

The next step involves the reduction of the 3-Carbon molecule into a Carbohydrate.

The final step is a complex series of reactions, which regenerates the 5-Carbon Acceptor (Ribulose-1-5-bisphosphate [RUBP]).



One CO_2 is gained with each cycle. Six cycles lead to the formation of a 6-Carbon sugar.

The Enzyme that adds CO_2 to RUBP is called RUBISCO (Ribulose Bisphosphate Carboxylase/Oxygenase). It is the *most abundant protein on the planet*. It can represent *40% of the soluble protein in a leaf*. 1

The Enzyme that adds CO_2 to RUBP is called RUBISCO (Ribulose Bisphosphate Carboxylase/Oxygenase). It is the *most abundant protein on the planet*. It can represent *40% of the soluble protein in a leaf*. *I wonder why!*

RUBISCO has a Dual Function. It can Carboxylate RUBP (above) or it can Oxygenate it. The latter is called Photorespiration.

Photorespiration results in the loss of CO_2 which *negates CO_2 fixation!*

Both of these reactions involve the same active site, and the substrates (CO_2 & O_2) directly compete with one another.

Under typical ambient conditions the ratio between CO_2 fixation & Oxygenation is 3:1.

Photorespiration reduces the efficiency of photosynthesis by as much as 50%. It is interesting to note that The dual nature of RUBISCO is universal from orchids to photosynthetic bacteria.

The Concentrations of CO_2 & O_2, plus the Leaf Temperature regulate the Balance between Carboxylation (Carbon Gain) & Oxygenation (Carbon Loss).

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The Concentrations of CO_2 & O_2, plus the Leaf Temperature regulate the Balance between Carboxylation (Carbon Gain) & Oxygenation (Carbon Loss).

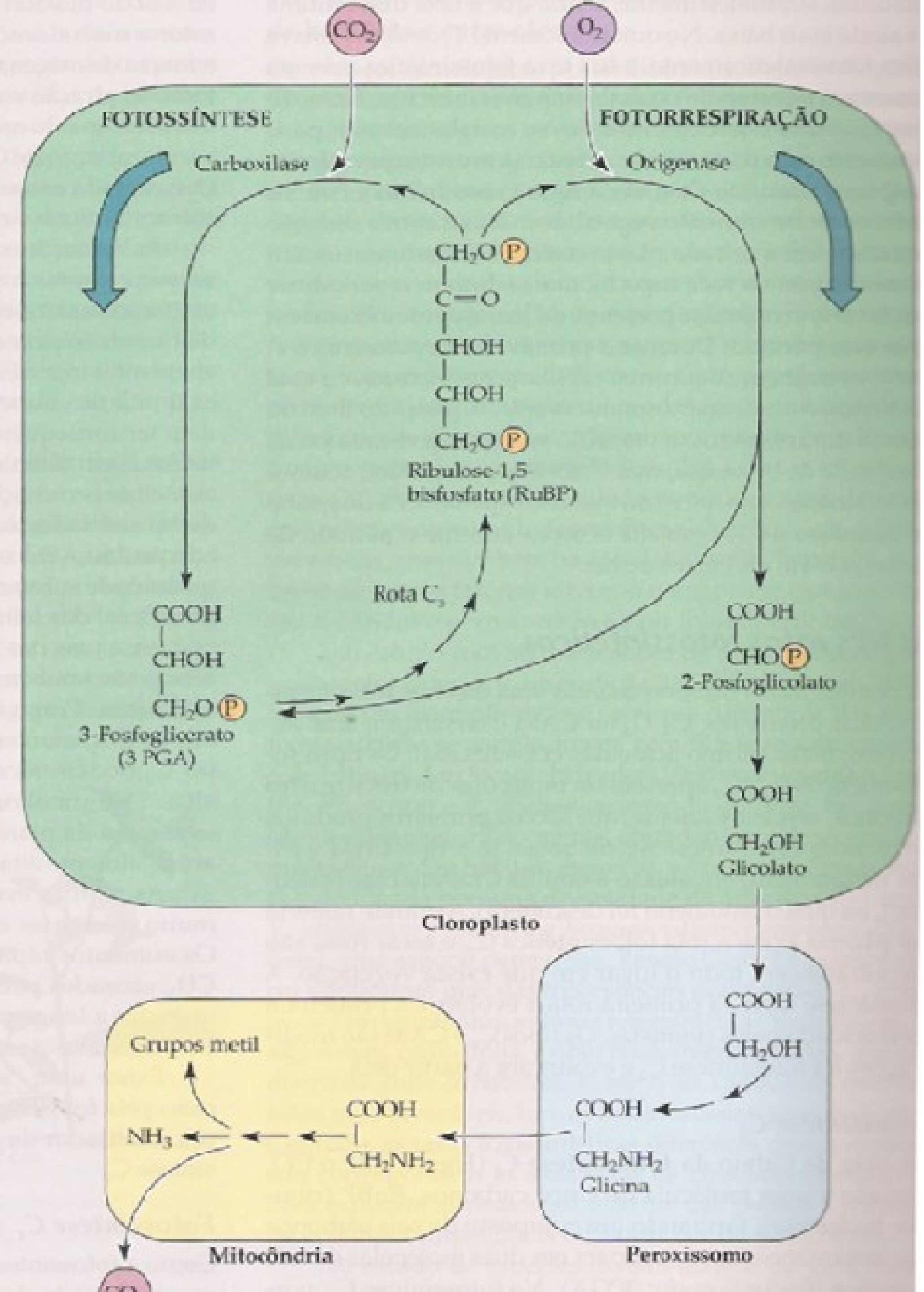
Carbon Dioxide concentrations are always much lower than Oxygen levels inside leaves and in the atmosphere.

Leaf Temperature rises during the day when photosynthesis occurs. This is especially true under dry, sunny conditions. This favors Oxygenation (Photorespiration).

The kinetic properties of RUBISCO also favor Oxygenation at high temperatures.

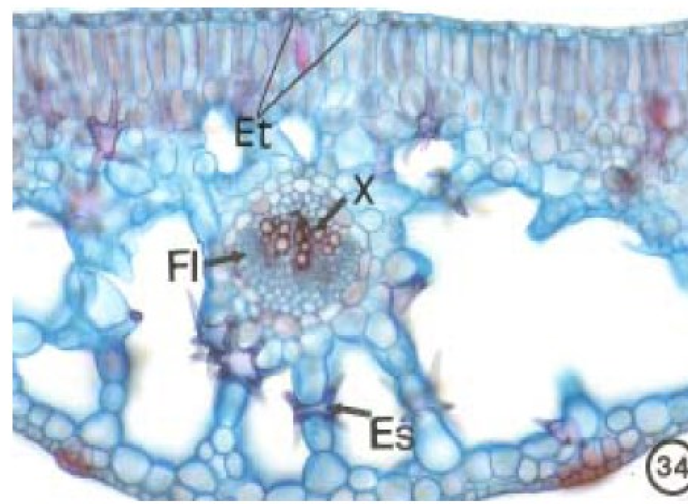
Elevated Temperatures favor Photorespiration
compared to CO_2 Fixation by Photosynthesis!

One way to favor Carboxylation over Oxygenation would be the Elevation of CO_2 levels in the vicinity of RUBISCO!

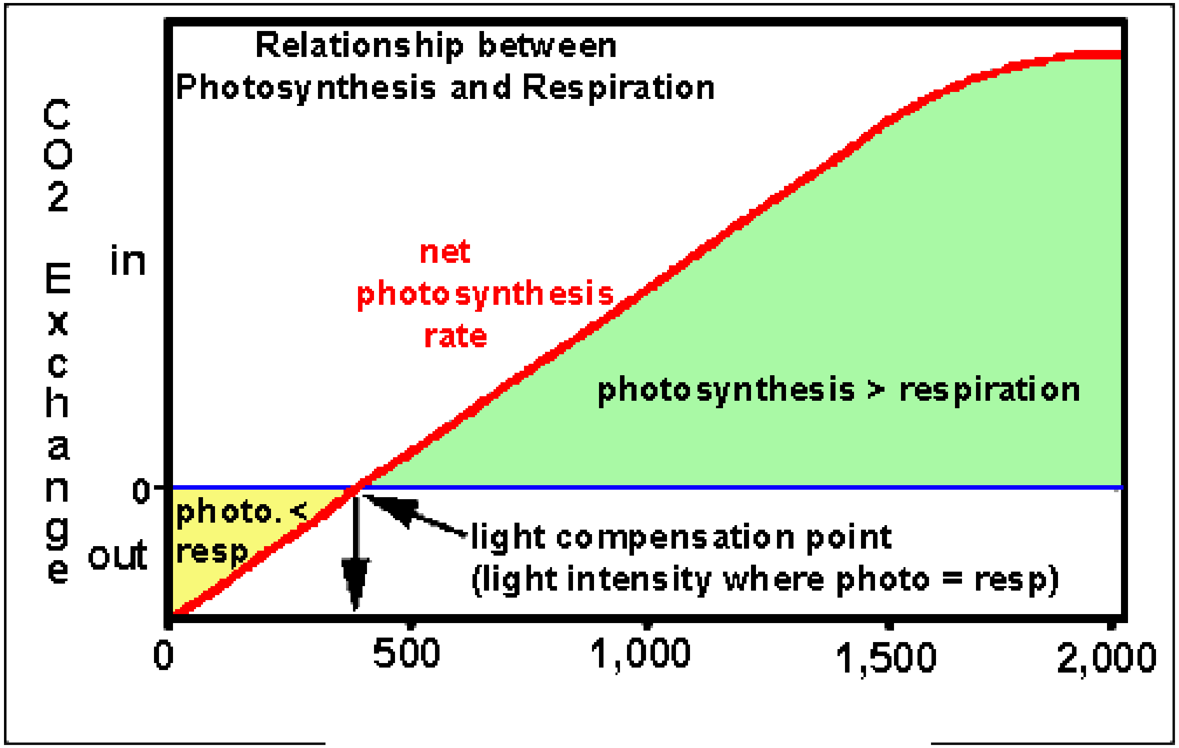


Folha C_3

Planta C_3



Nymphoides indica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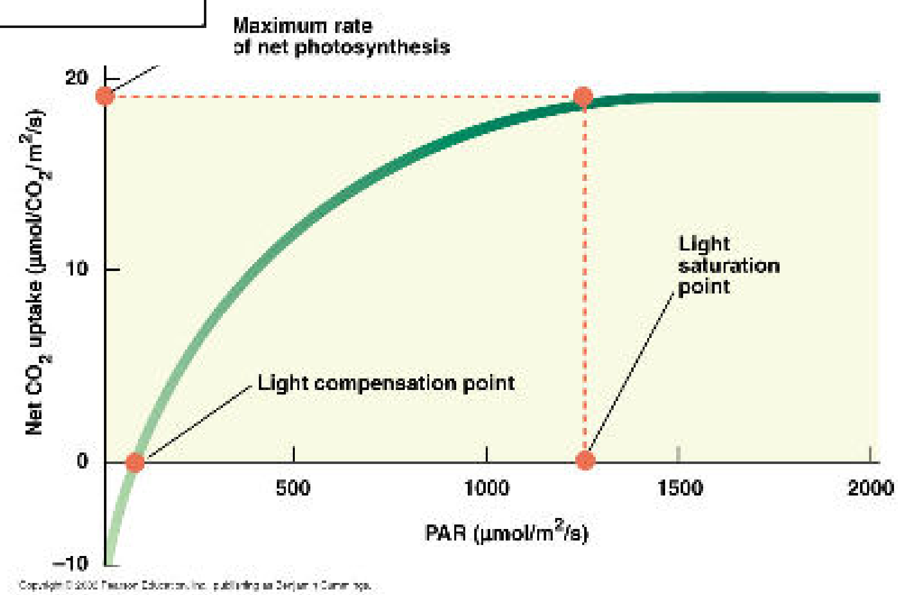

Maximum rate
of net photosynthesis
Net CO2 uptake (µmol/CO2/m2/s)
20
10
0
−10
Light
saturation
point
Light compensation point
500
1000
1500
2000
PAR (µmol/m2/s)

Evapo/Transpiration is the principal way in which leaves cool themselves.

The latent heat of evaporation produces a significant cooling effect.

This occurs best when the stomata are open.

However, leaf water loss leads to stomatal closure.

Since water loss is greatest when leaf temperatures are the highest, the stomata are typically closed under these circumstances. This greatly limits evaporative cooling!

Closed stomata also prevent CO_2 uptake from the atmosphere.

All of these factors favor Photorespiration &

Diminish Photosynthesis!

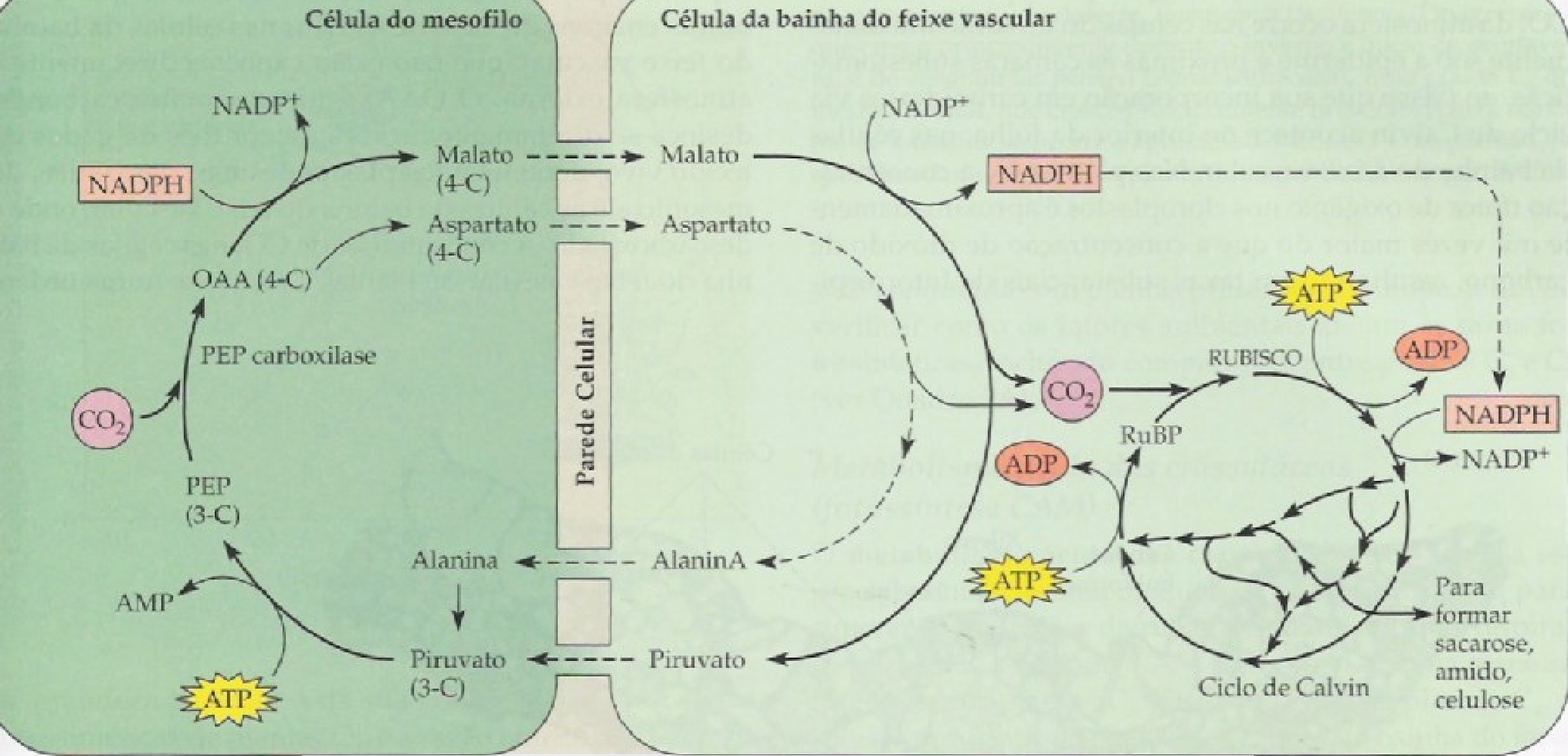
Some plants have Carboxylating enzymes that have a higher affinity for CO_2, compared to RUBISCO, especially at low CO_2 concentrations & high temperatures.

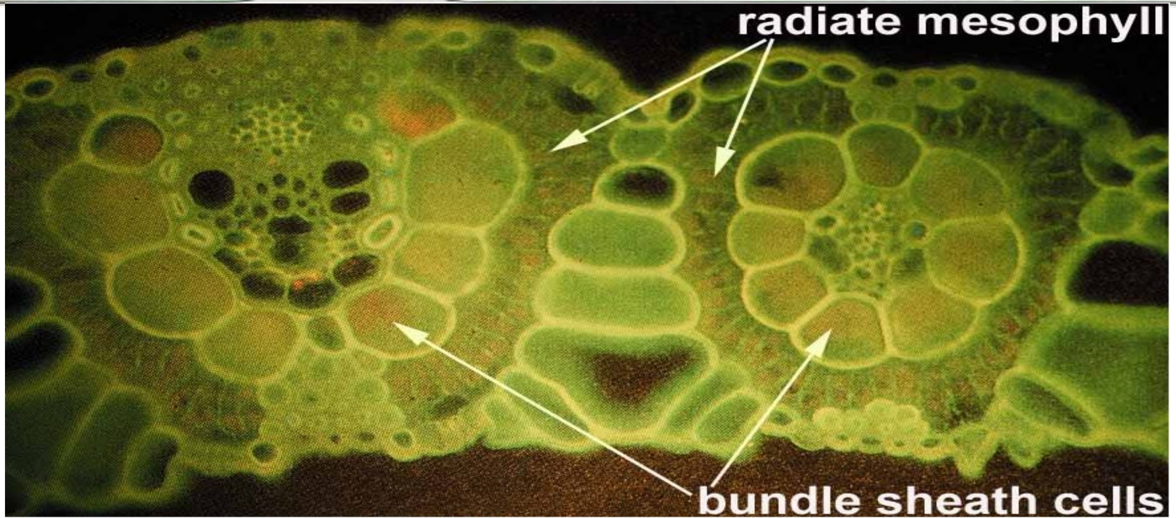
These plants use 3-Carbon acceptors like Phosphoenolpyruvate (PEP) rather than the 5-Carbon acceptor RUBP.

Carboxylation produces a 4-Carbon Acid like Malic Acid (Malate).

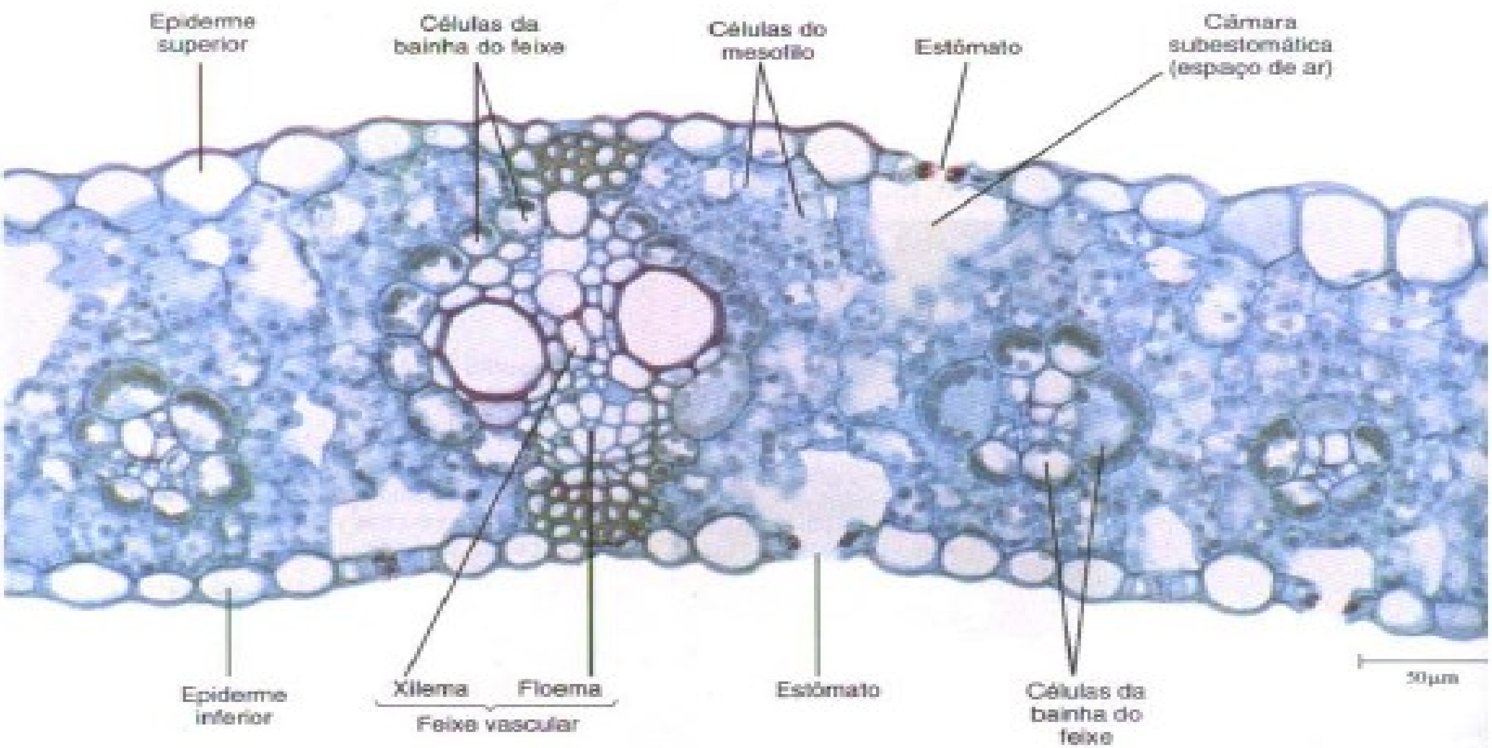
Consequently, this is called C4 photosynthesis.

C4 Plants have a distinctive Leaf Anatomy compared to C3 Plants.


Célula do mesofilo
Célula da bainha do feixe vascular
NADP+
NADPH
Malato
(4-C)
Aspartato
(4-C)
OAA (4-C)
PEP carboxilase
CO2
PEP
(3-C)
AMP
ATP
Alanina
Piruvato
(3-C)
Parede Celular
Malato
Aspartato
AlaninA
Piruvato
NADP+
NADPH
ATP
ADP
RUBISCO
CO2
RuBP
ADP
ATP
NADPH
NADP+
Ciclo de Calvin
Para
formar
sacarose,
amido,
celulose

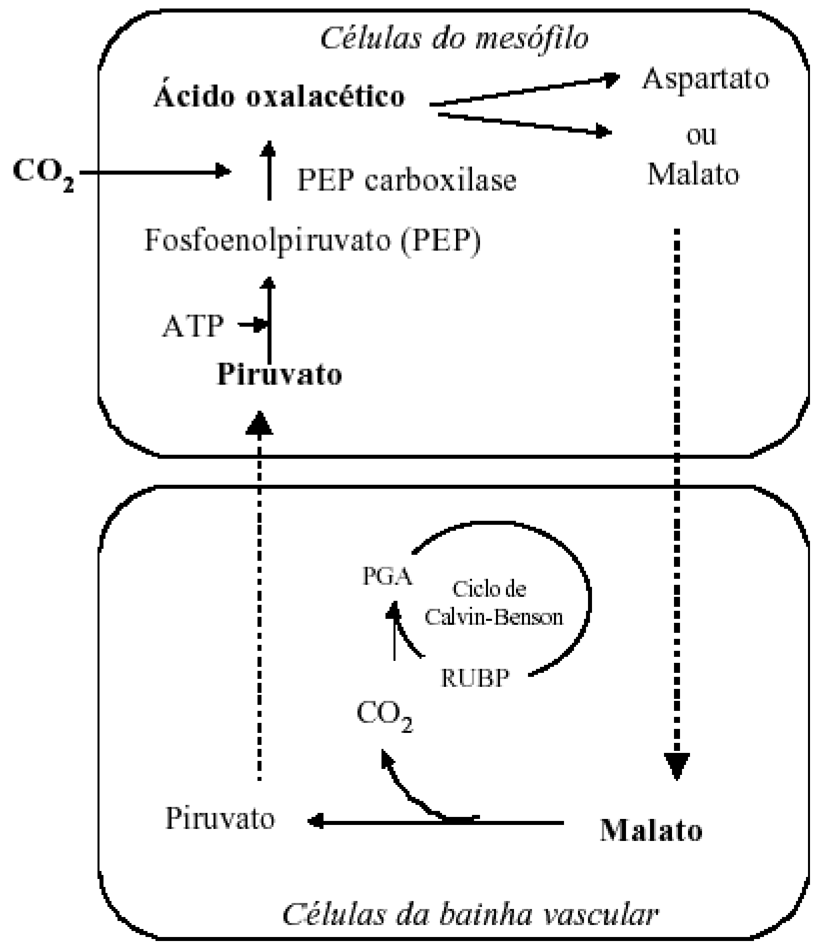

radiate mesophyll
bundle sheath cells

Estrutura Kranz

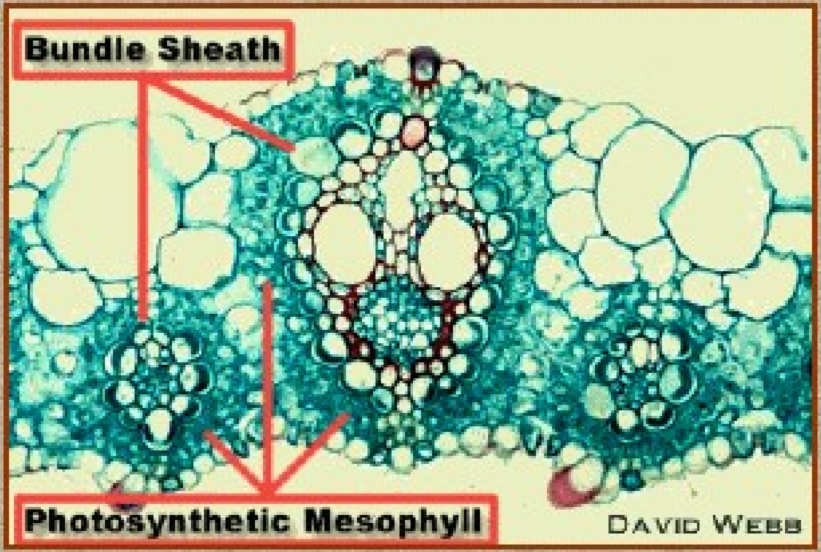


Zea mays

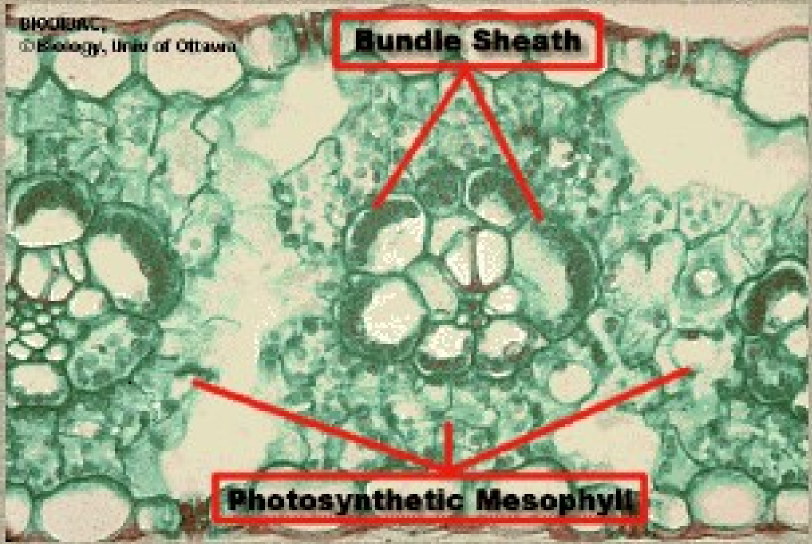
Raven 2001


Células do mesófilo
Ácido oxalacético
Aspartato
ou
Malato
CO2
PEP carboxilase
Fosfoenolpiruvato (PEP)
ATP
Piruvato
PGA
Ciclo de
Calvin-Benson
RUBP
CO2
Piruvato
Malato
Células da bainha vascular

The picture on the right is from Sugarcane (Saccharum) which has C4 Photosynthesis & Kranz Anatomy. Note the large Photosynthetic Bundle Sheath Cells and the densely stained, Photosynthetic Mesophyll that surround the Bundle Sheath.



The picture on the right is from a grass in the genus Poa. It also has Kranz Anatomy & C4 Photosynthesis Note the Chloroplasts in the Bundle Sheath Cells. The Stomata are precisely arranged to provide optimal diffusion paths for the Photosynthetic Mesophyll Cells. This allows for extremely efficient gas exchange with the atmosphere and the Mesophyll when the stomata are open.



This C4 process is more efficient than C3 photosynthesis because

PEP Carboxylase has a much higher affinity for CO_2 than RUBISCO.

PEP Carboxylase does NOT have Oxygenase activity.

The CO_2 concentration in the Bundle Sheath Chloroplasts greatly favors Carboxylation by RUBISCO & virtually eliminates Photorespiration.

The Energy for this process comes from the Chloroplasts in the Mesophyll Cells which produce lots of ATP and NADPH.

C4 Carbon Fixation requires more energy than C3 photosynthesis. However, the increased efficiency of CO_2 fixation far outweighs the increased energy requirements.

C4 plants photosynthesize better than C3 plants under dry, hot conditions.

The greater affinity of PEP Carboxylase for its substrate means that the enzyme is saturated at low ambient CO_2 levels.

Consequently, stomata may be closed for longer periods of time with C4 plants. This obviously helps to conserve water.

C4 plants are more abundant in hot arid climates, as might be expected.

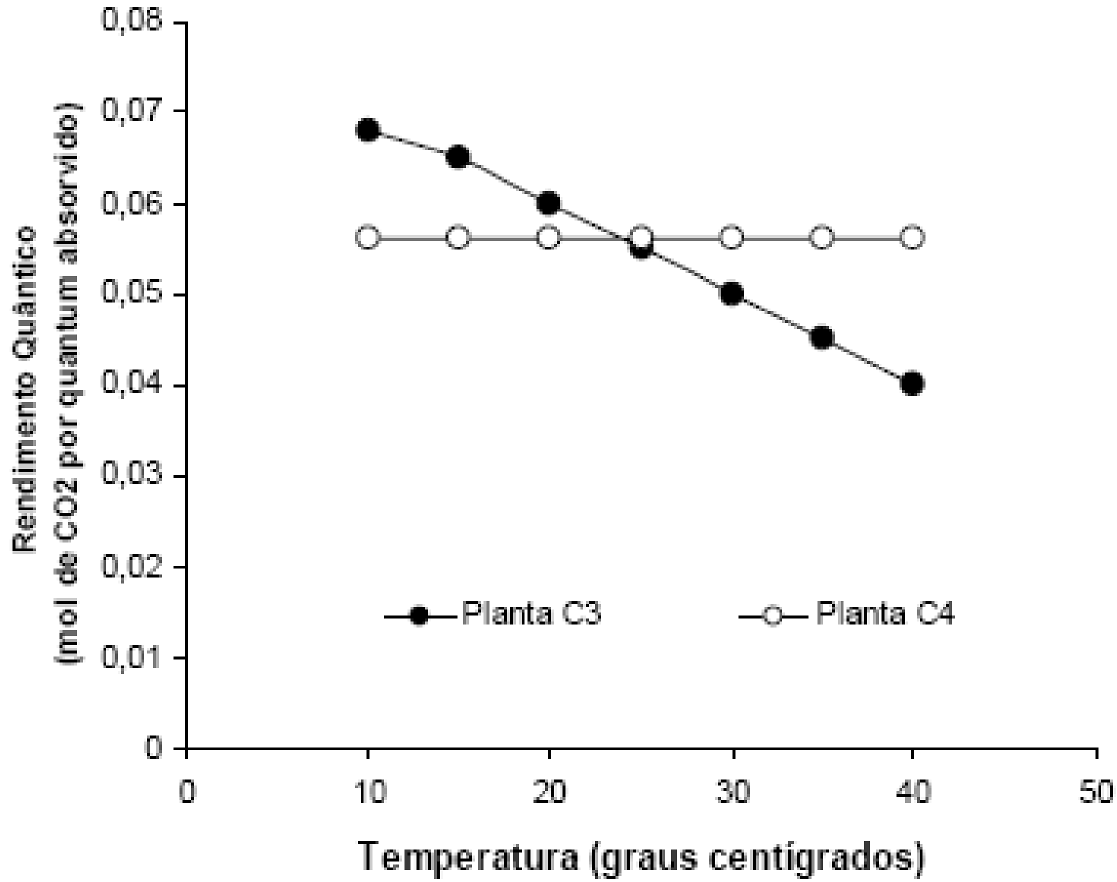


Figura 2. Rendimento comparado de plantas C3 e C4

Plant type	C3	C4
Economically Important Species	wheat, rice, barley, potato	maize, sugar cane, millet
Leaf anatomy	Pallisade and spongy mesophyll, if bundle sheath present no chloroplasts	Kranz anatomy with bundle sheath containing chloroplasts
Chloroplasts	1 type	2 types (dimorphic)
Primary Carboxylase	Rubisco	PEPCase in mesophyll
Secondary Carboxylase	None	Rubisco separated in space (bundle sheath)
Primary CO_2 acceptor	RuBP	PEP
1st stable product	3-phosphoglyceric acid (3-PGA)	oxalacetate (OAA)
CO_2:ATP:NADPH	1:3:2	1:5:2
Transpiration rate	high	~25% of C3
light compensation point	5 Wm-2	< 1 Wm-2
photorespiration rate	High (30% of net photosynthesis)	low to undetectable
Optimum temperature	25	35
Productivity (tonnes/ha/yr)	~20	~30

About 3000 species of C4 plants have been recorded from some 18 families of flowering plants. Some C4-plants of economical importance are sugar cane, ma and sorghum. In general, C4-plants are thought to have evolved under conditions of high temperatures and lower CO_2 concentrations *(review in Black, 1994)* thus many C4-species are from the tropics. Characteristically, C4-plants have higher rates of photosynthesis than C3-plants. Photosynthesis in C4 plants does saturate but increases at high light intensities and can continue at very low CO_2 concentrations. Subsequently, these plants have rapid growth rates and higher biomass and economic yields than C3-plants.

The observed increases in both global temperatures and in the atmospheric concentrations of carbon dioxide (CO_2) could have profound effects on primary production for both "wild" and cultivated species. Higher temperatures and higher CO_2 concentrations could mean higher total primary production by increasing both the geographical areas of plant growth as well as higher photosynthetic rates for individual species. Interspecific interactions and competition would favor species adapted to high temperatures and resistant to low water levels. These populations could subsequently "migrate" or be introduced to new habitats and succeed other plants that cannot survive such conditions. Additionally, the increase in primary production could then modify important biogeochemical cycles su as the carbon, oxygen, and nitrogen cycles **(Figure 4).**

Sage says that during the early Eocene epoch, around 50 million years ago, CO_2 levels in the atmosphere went into a gradual decline, and by the early Miocene, around 25 million years ago, reached 280ppm - around the same concentration as in recent, pre-industrial times.

The first C4 plants appeared around 30 million years ago, and underwent explosive evolutionary radiation around 25 million years ago. Whether the primary selective pressure was increasing aridity, or lowering CO_2 levels, is still debated.

But the outcome was that C4 plants were more efficient than their C3 ancestors in drier, low-CO_2 conditions because they evolved a novel anatomical solution to the photorespiration problem.

Grasses constitute around half of the world's 14,000-odd C4 plants, and 25 per cent are sedges. Within the grass family, the trait has evolved about 15 times; among sedges, four times.

Although dicots account for only 15 per cent of C4 taxa, the trait has evolved up to 35 times - Sage says most C4 dicots are herbs and shrubs, with a small minority of woody trees.

This pattern of multiple evolution of C4 photosynthesis suggests the process is ongoing: that there should be possible to catch plants in the evolutionary act of evolving the trait.

"We determine the [independent] origins of C4 by analysising phylogenetic patterns, and we find it popping up in different lineages," he says.

"In a few lineages, we've gone in and looked at individual species, and found traits indicative of change from C3 to C4 photosynthesis.

Crassulacean Acid Metabolism (CAM) is another ecologically significant way in which plants concentrate CO_2.

This does not involve the sophisticated structural specialization seen with C4 plants.

Stomatal opening is regulated temporally so that they may *Open at Night* when water demand is low, thus avoiding water loss.

CAM plants can show an 80% reduction in water loss compared to C3 plants under the same conditions. This has obvious adaptive and ecological significance!

CAM plants open their stomata at night and fix CO_2 via PEP Carboxylase (a la C4 photosynthesis).

They Store Malate (4 Carbon Acid) in their Vacuoles.

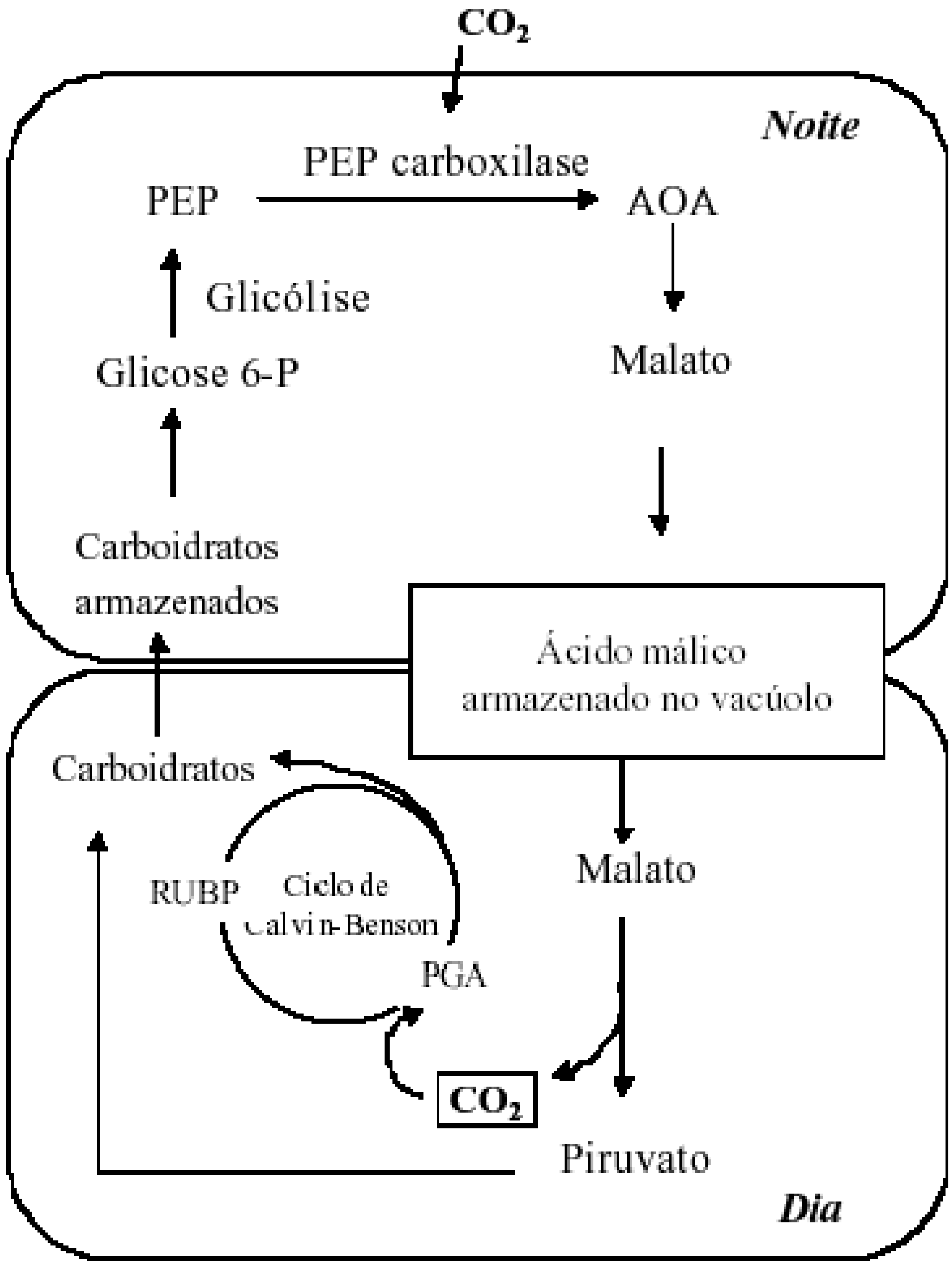
Malate is transported to Chloroplasts during the Day where Decarboxylation occurs.

The released CO_2 is Fixed by RUBISCO as in C3 plants.

CAM Mesophyll Cells typically have extremely Large Storage Vacuoles and CAM Plants are Often Succulent in appearance.

Since the Stomata are Closed during the Day, CO_2 & Water can't escape.

Virtually all of the CO_2 is fixed and Photorespiration is negligible.

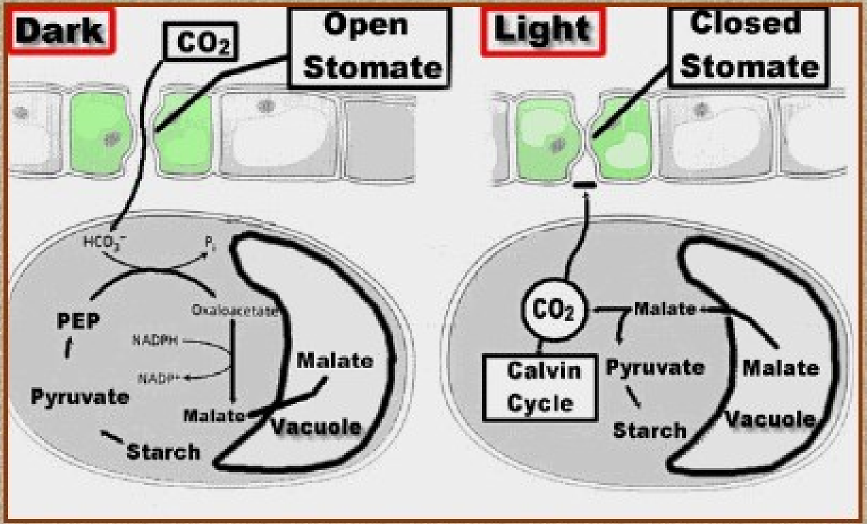


CO_2
Noite
PEP carboxilase
PEP
AOA
Glicólise
Glicose 6-P
Malato
Carboidratos armazenados
Ácido málico armazenado no vacúolo
Carboidratos
Malato
RUBP
Ciclo de Calvin-Benson
PGA
CO_2
Piruvato
Dia

Stomata of CAM plants are closed during the day.

The Stomata open at night and atmospheric CO_2 enters the leaf.

It is fixed by PEP Carboxylase and converted to Malate which accumulates in the Vacuole.

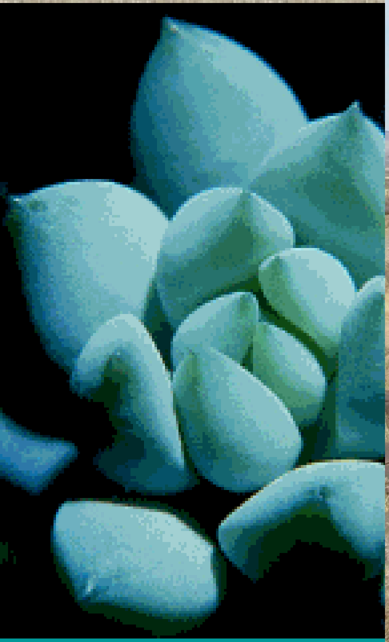


Malate is transported from the Vacuole and Decarboxylated.

The released CO_2 can't escape because the stomata are closed.

Virtually all of the CO_2 is fixed by the Calvin (C3) Cycle.

CAM photosy
families like the Cr
Sedum), Aizoaceae
Euphorbiaceae. How
species. Some famili
Pineapple (Bromeliac
Orchids (Orchidacea
adapted to cope w
photosynthesis is c
adaptations.



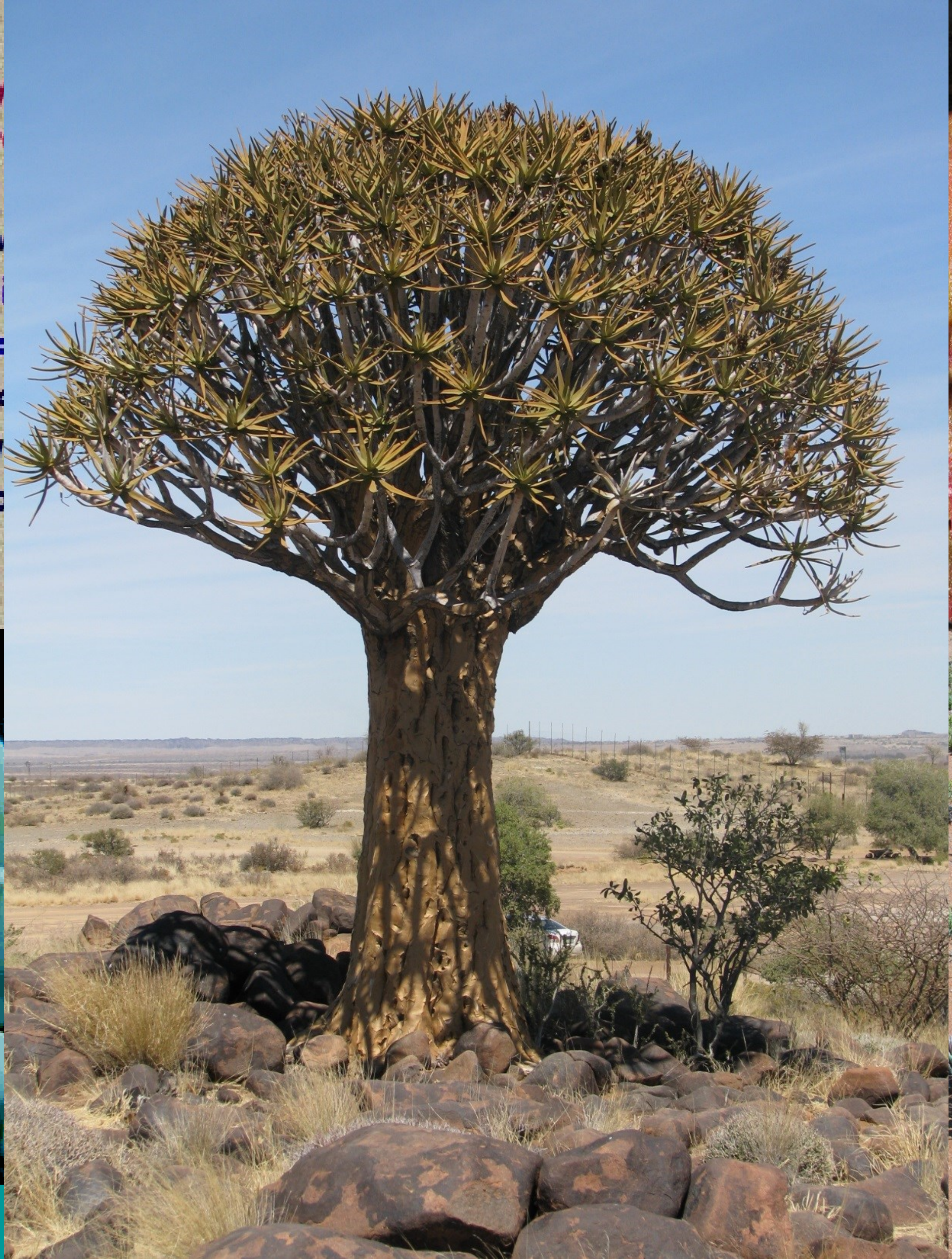
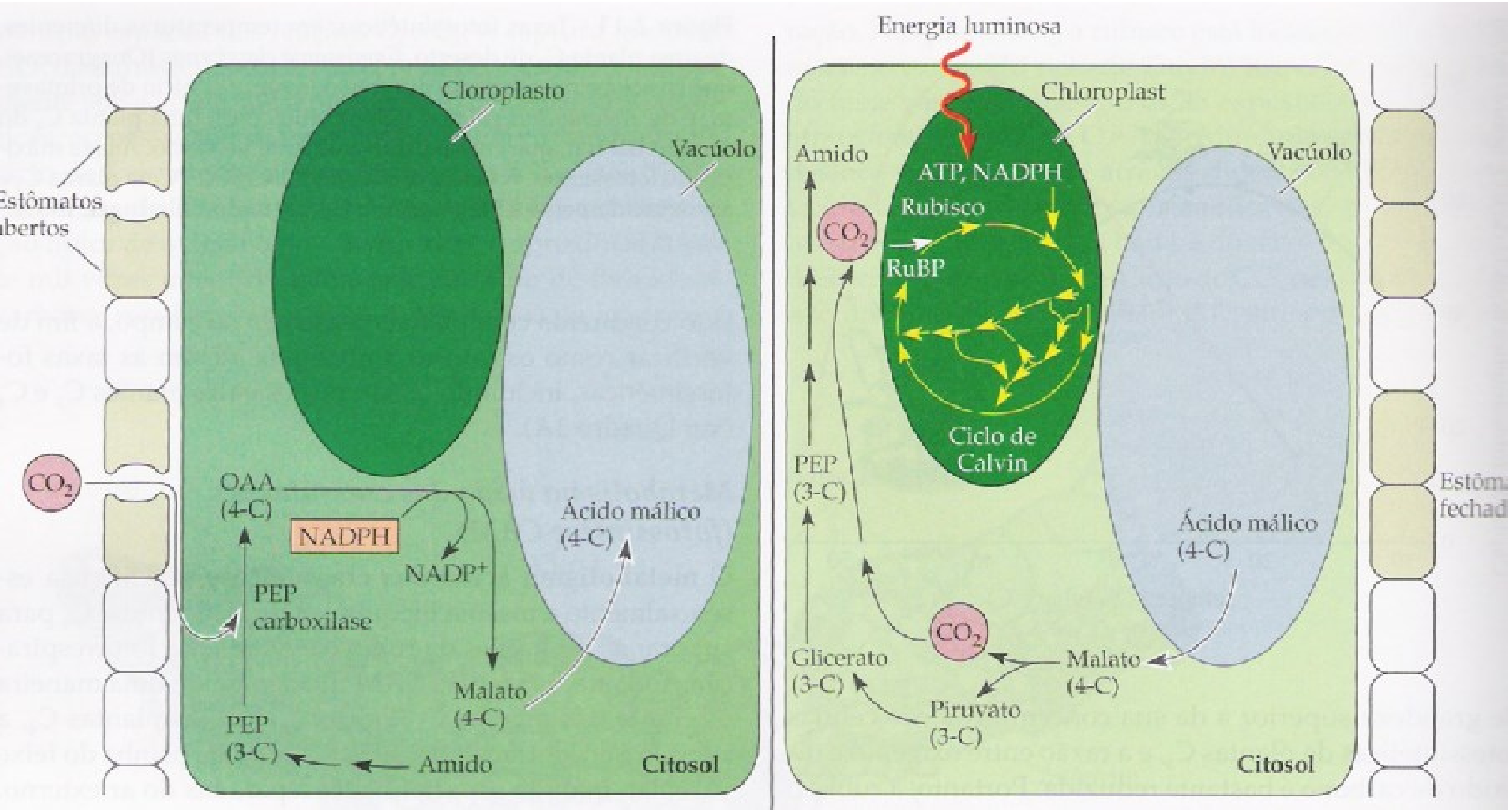


TABLE 11. Taxonomic survey of flowering plant families known to have species showing crassulacean acid metabolism (CAM) in different taxa.

Agavaceae	Geraniaceae
Aizoaceae	Gesneriaceae
Asclepidiaceae	Labiatae
Asteraceae	Liliaceae
Bromeliaceae	Oxalidaceae
Cactaceae	Orchidaceae
Clusiaceae	Piperaceae
Crassulaceae	Polypodiaceae
Cucurbitaceae	Portulacaceae
Didieraceae	Rubiaceae
Euphorbiaceae	Vitaceae

Source: Kluge & Ting (1978) and Medina (1996).



Estômatos
abertos
CO2
Cloroplasto
Vacúolo
OAA
(4-C)
NADPH
NADP+
PEP
carboxilase
Ácido málico
(4-C)
Malato
(4-C)
PEP
(3-C)
Amido
Citosol
Energia luminosa
Chloroplast
Amido
ATP, NADPH
Rubisco
CO2
RuBP
Vacúolo
Ciclo de
Calvin
PEP
(3-C)
Ácido málico
(4-C)
CO2
Glicerato
(3-C)
Malato
(4-C)
Piruvato
(3-C)
Citosol

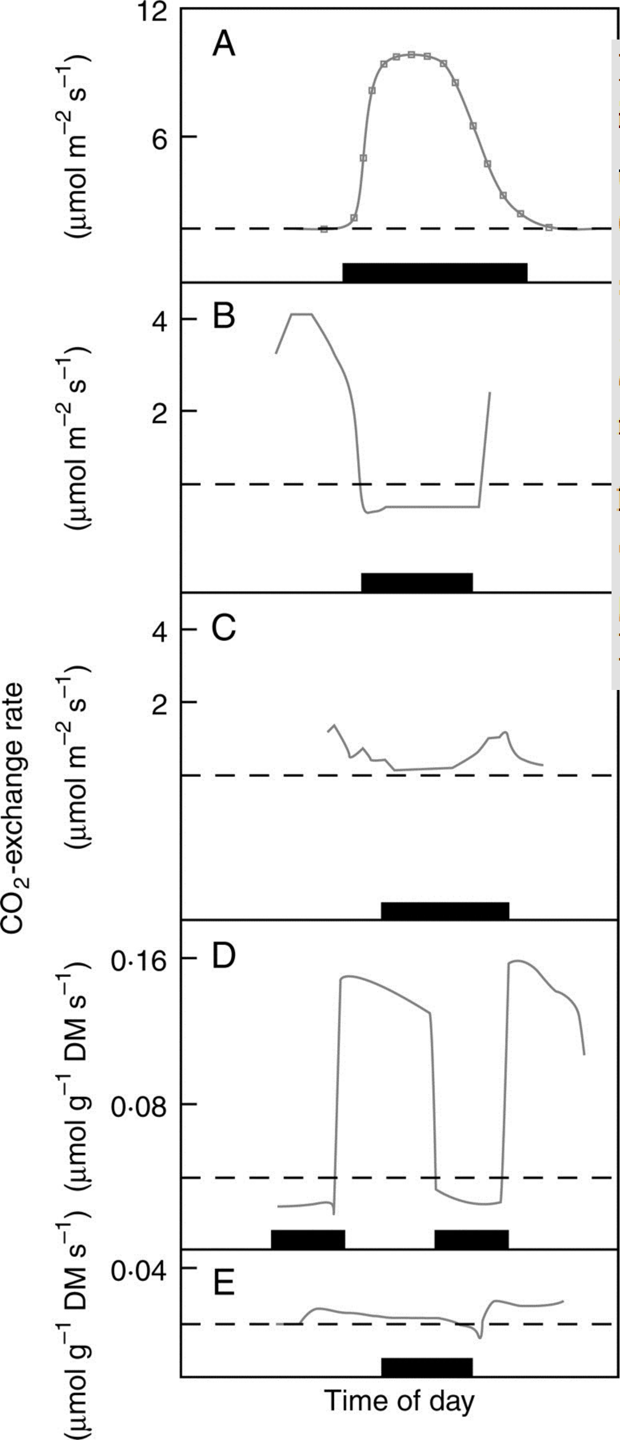
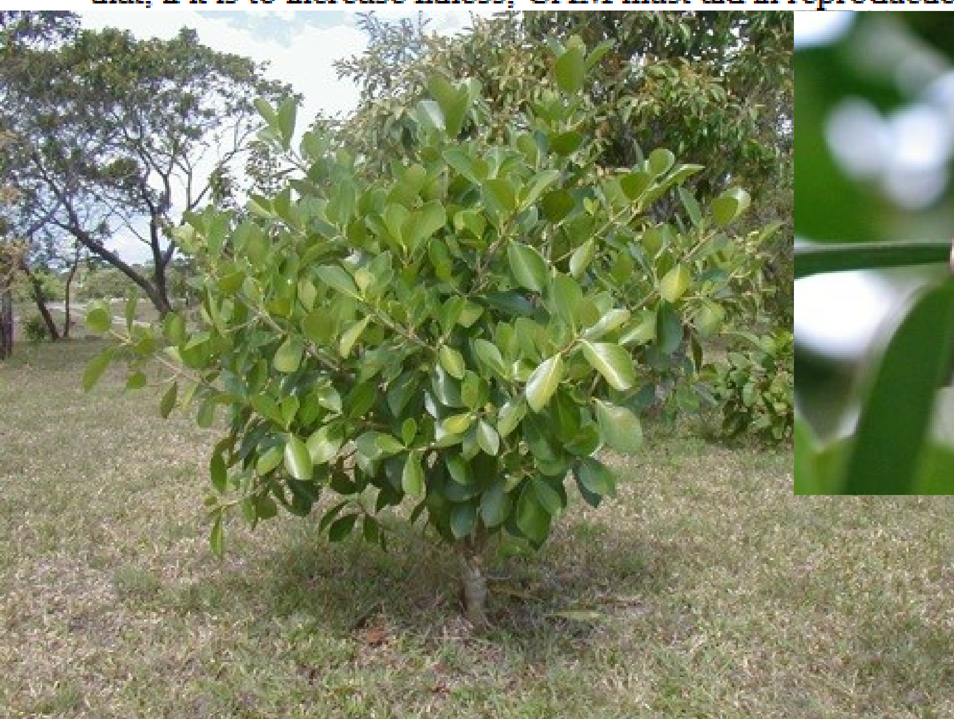


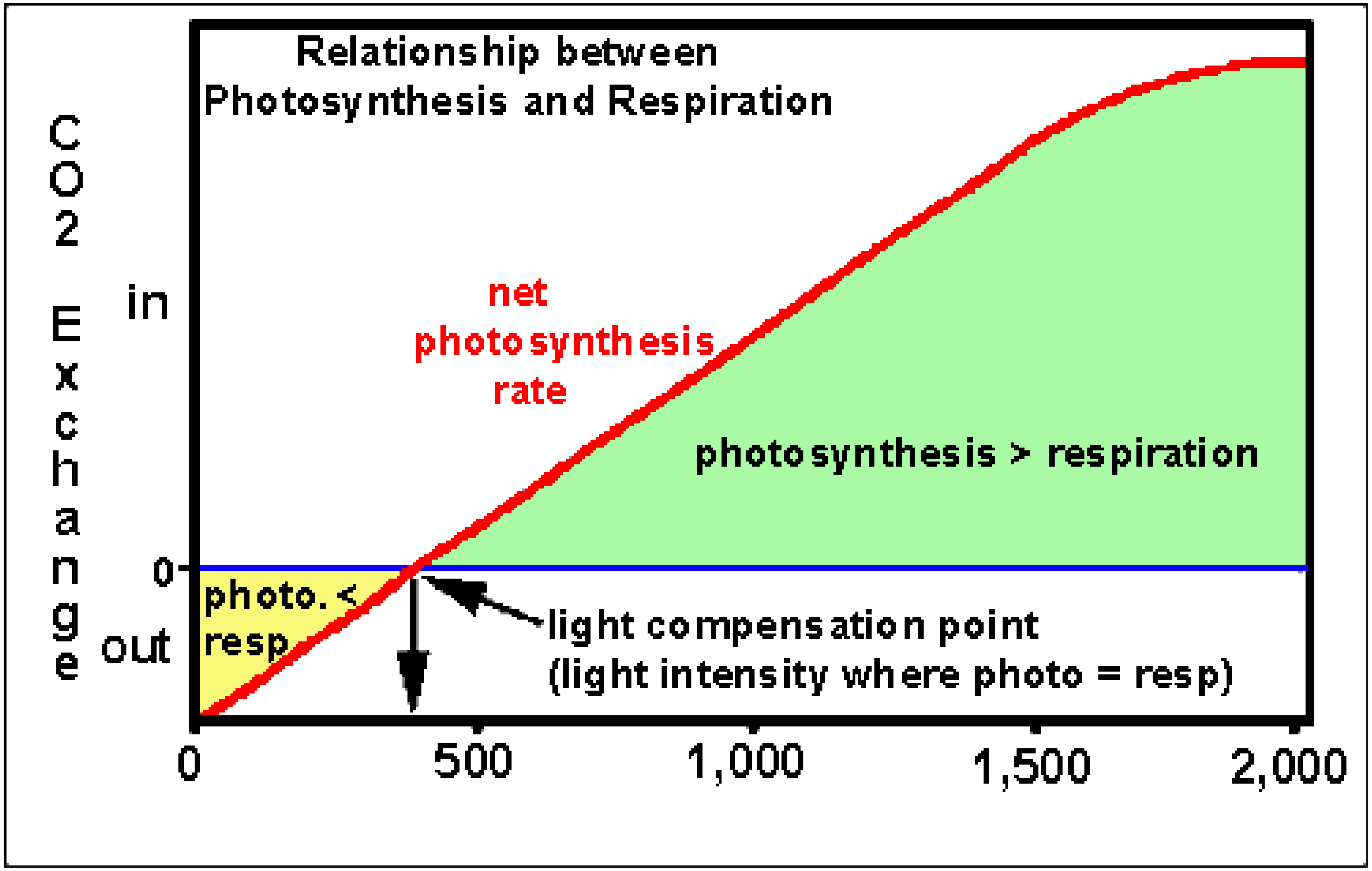
FIG. 1. Daily gas-exchange of plants with different modes of CAM: (A) Obligate CAM in watered plants of *Opuntia ficus-indica* (Nobel and Hartsock, 1983); (B) C_3 CO_2-uptake in well-watered plants of the inducible-CAM species, *Talinum triangulare* (Herrera *et al.*, 1991); (C) small dark CO_2 fixation in plants of *T. triangulare* drought-stressed for 10 d (Herrera *et al.*, 1991); (D) CAM-cycling in watered plants of *Talinum calycinum* (Martin *et al.*, 1988); (E) CAM-idling in plants of *Talinum calycinum* drought-stressed for 3 d (Martin *et al.*, 1988). The broken line indicates no net CO_2-exchange; the dark bar on the abscissa indicates the duration of the dark period. The corresponding values of nocturnal acid accumulation were: (A) 85 μmol H^+ cm^{-2} (droughted plants had a value of 16 μmol H^+ cm^{-2}); (B) 8 μmol H^+ g^{-1} FM (0·2 μmol H^+ cm^{-2}); (C) 100 μmol H^+ g^{-1} FM (2·0 μmol H^+ cm^{-2}); (D, E) 56 μmol H^+ g^{-1} FM. Redrawn with permission from the authors.

Herrera, A. Ann Bot 2009 103:645-653; doi:10.1093/aob/mcn145

Background: In obligate Crassulacean acid metabolism (CAM), up to 99 % of CO_2 assimilation occurs during the night, therefore supporting the hypothesis that CAM is adaptive because it allows CO_2 fixation during the part of the day with lower evaporative demand, making life in water-limited environments possible. By comparison, in facultative CAM (inducible CAM, C_3-CAM) and CAM-cycling plants drought-induced dark CO_2 fixation may only be, with few exceptions, a small proportion of C_3 CO_2 assimilation in watered plants and occur during a few days. From the viewpoint of survival the adaptive advantages, i.e. increased fitness, of facultative CAM and CAM-cycling are not obvious. Therefore, it is hypothesized that, if it is to increase fitness, CAM must aid in reproduction.



Clusia


Relationship between
Photosynthesis and Respiration
CO2 Exchange
in
out
0
net
photosynthesis
rate
photosynthesis > respiration
photo. <
resp
light compensation point
(light intensity where photo = resp)
0
500
1,000
1,500
2,000