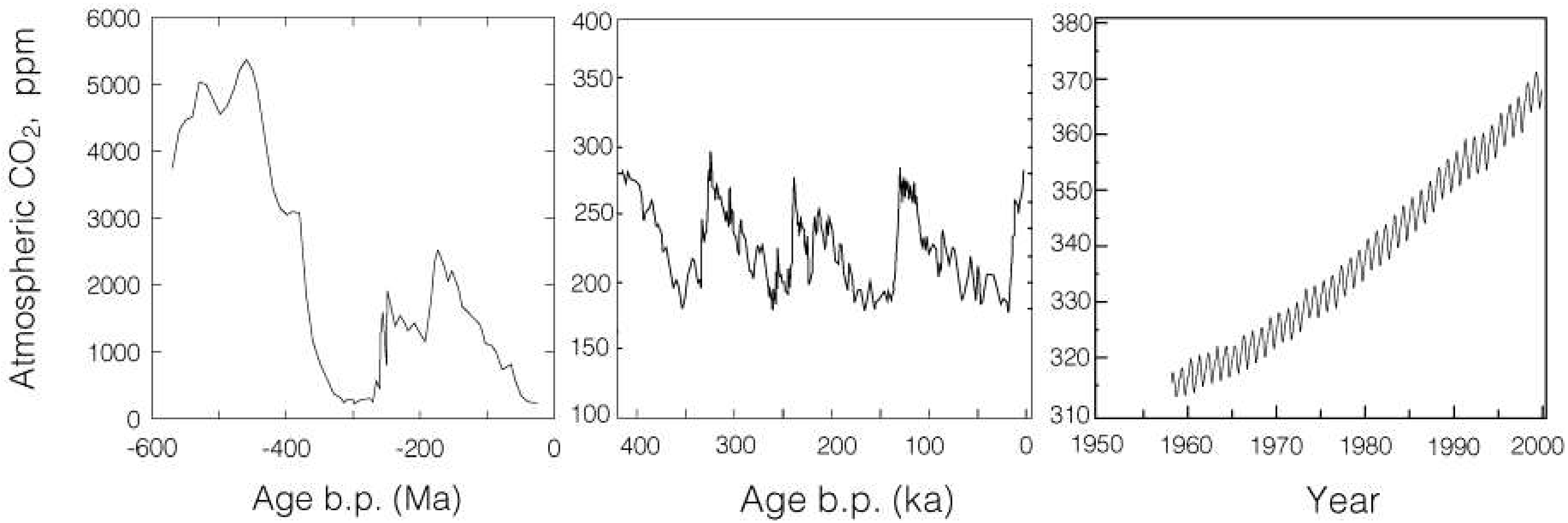
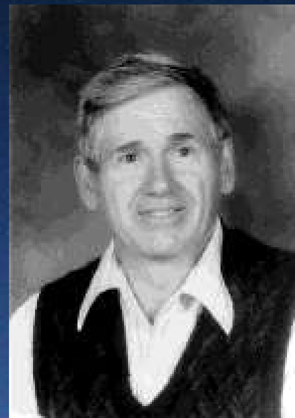
A CO_2 history of our planet . . . . .



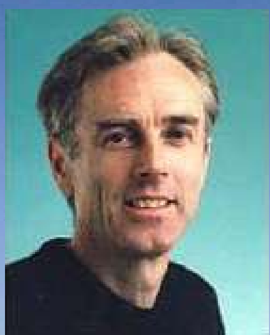
Harmon Craig



Dave Keeling

Graham Farquhar

Joe Berry



Pieter Tans

Philippe Ciais

Bruce Smith

Marion O'Leary

Dan Yakir

IsoHistory - - - pioneers in the field

Standard delta notation

$$\delta = \frac{R_{plant}}{R_{standard}} - 1$$

We then multiply by 1000 to get to familiar "per mil" unit

Defining isotope effect and discrimination

$$\alpha = \frac{R_{air}}{R_{plant}}$$

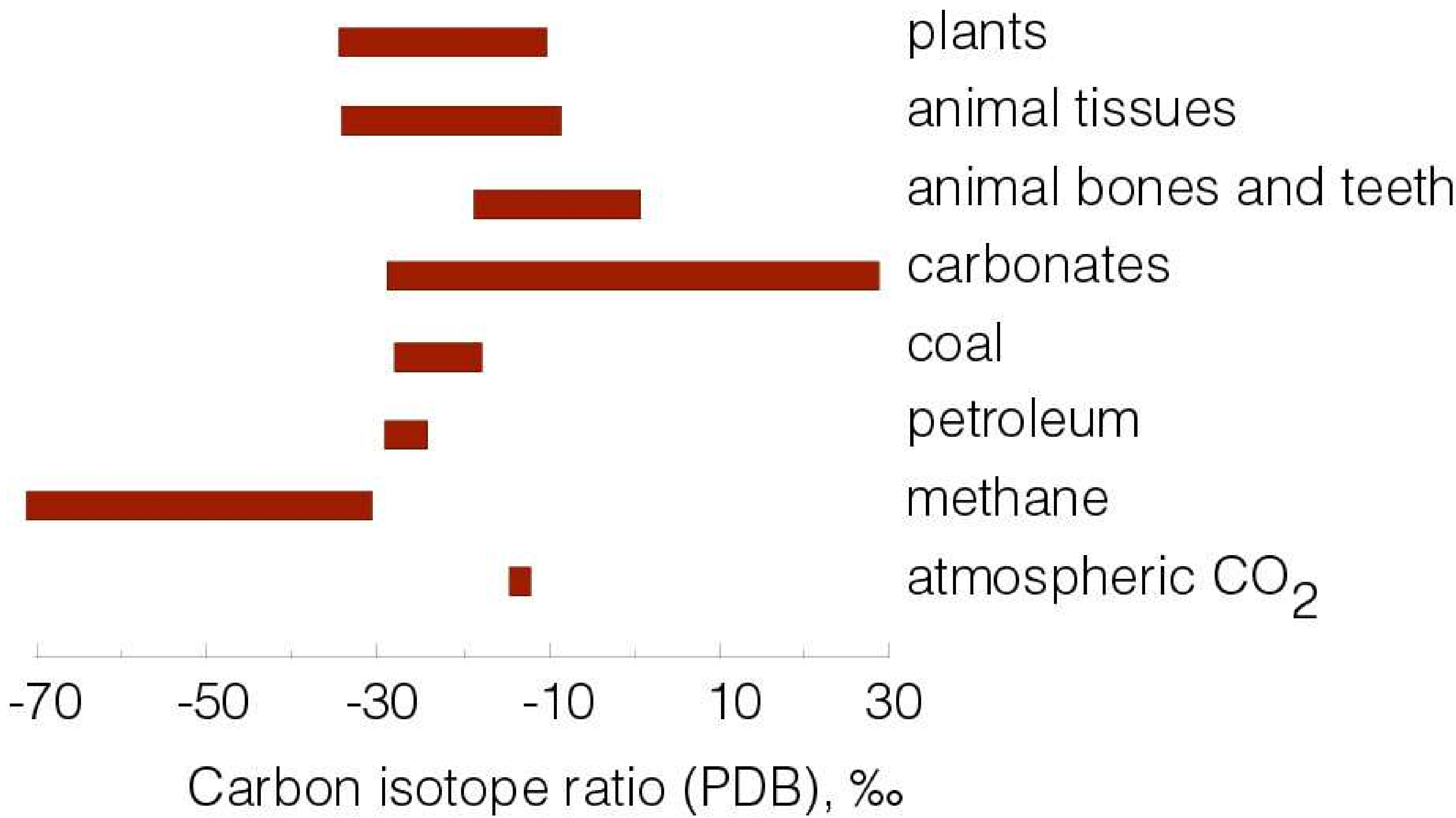
$$\Delta = \alpha - 1 = \frac{R_{air}}{R_{plant}} - 1$$

We can express ^{13}C composition in "delta" or "discrimination" notation

$$\delta = \frac{R_{plant}}{R_{standard}} - 1$$

$$\Delta = \frac{\delta_{air} - \delta_{plant}}{1 + \delta_{plant}}$$

What is the typical range of δ values for plant tissues?



Variations in ^{13}C are associated with photosynthetic pathway

C_3

C_4

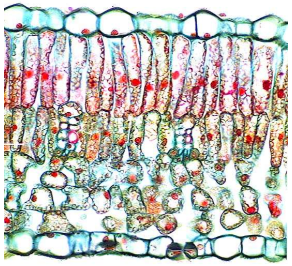
> 95 % of all plant species
70-75 % of all productivity (today)
~ 50 % of all productivity (ice age)

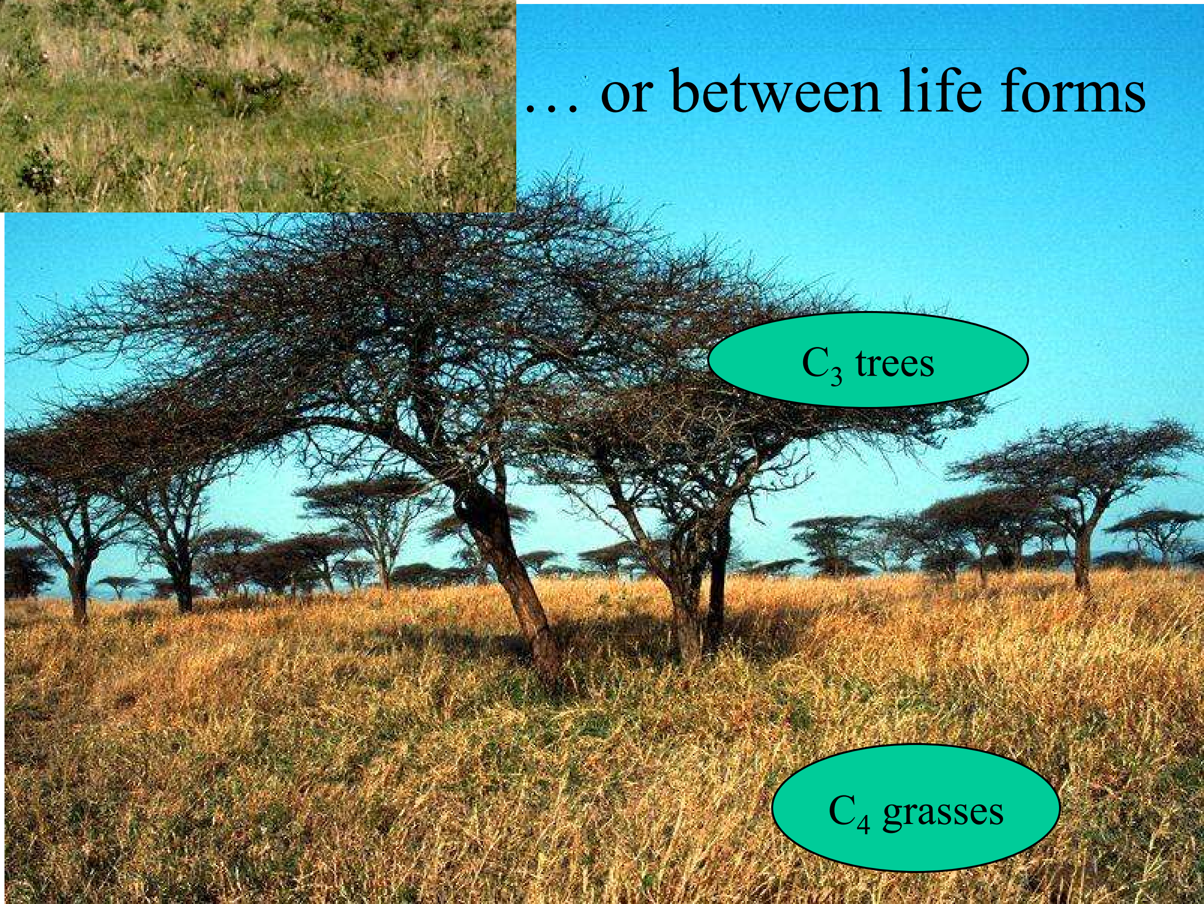
< 5 % of all plant species
25-30 % of all productivity (today)
~ 50 % of all productivity (ice age)

herbivores often exhibit feeding preference for C_3 versus C_4 leaves

Compare within a life form ...

… or between life forms



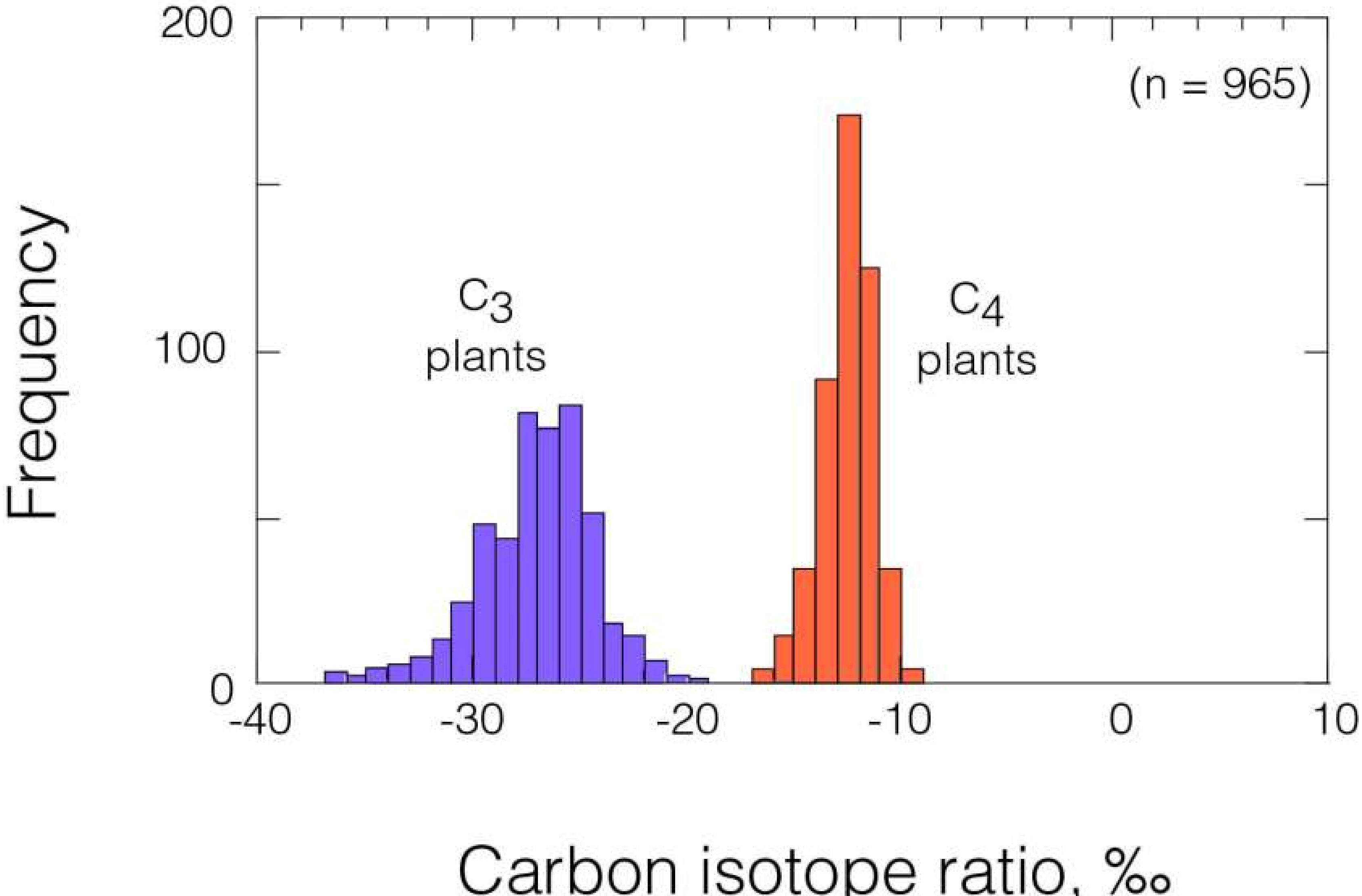


Common C_3/C_4 landscapes

C_3 trees

C_4 crops and grasses

C_3 and C_4 plants differ in their carbon isotope ratios



Cerling et al (1997)

C_4 present only in advanced angiosperms

Available data suggest multiple, independent evolution events

Families known to possess the C_4 photosynthetic pathway

- Acanthaeceae
- Aizoaceae
- Amaranthaceae
- Boraginaceae
- Capparidaceae
- Caryophyllaceae
- Chenopodiaceae
- Cleomaceae
- Compositae
- Cyperaceae
- Euphorbiaceae
- Gramineae
- Nyctaginaceae
- Polygonaceae
- Portulacaceae
- Scrophulariaceae
- Zygophyllaceae

Two primary groups within Angiosperms contain different abundances of C_3 and C_4 species

	C_3 species	C_4 species
Monocots	~ 6,000	~ 6,000
Dicots	~ 300,000	~ 2,000

While C_4 is widespread among families, it typically occurs in only a few genera per family.

<u>Dicotyledonae</u> (Subclass)

Caryophylles (Order)		
	Aizoaceae	*Cypselea, Gisekia, Trianthema, Zalaeya*
	Amaranthaceae	*Acanthochiton, Aerva, Alteranthera, Amaranthus, Brayulinea, Froelichia, Gomphrena, Gossypianthus, Lithophila, Tidestromia*
	Caryophyllaceae	*Polycarpaea*
	Chenopodiaceae	*Atriplex, Bassia, Halogeton, Haloxylon, Kochia, Salsola, Suaeda, Theleophyton*
	Molluginaceae	*Glinis, Mollugo*
	Nyctaginaceae	*Allionia, Boerhaavia, Okenia*
	Portulaceae	*Portulaca*
Polygonales (Order)		
	Polygonaceae	*Calligonum*
Euphorbiales (Order)		
	Euphorbiaceae	*Chamaesyce, Euphorbia*
Brassicales (Order)		
	Capparaceae	*Gynandropsis*
Linales (Order)		
	Zygophyllaceae	*Kallstroemia, Tribulus, Zygophyllum*
Asterales (Order)		
	Asteraceae	*Flaveria, Isostigma, Glossocordia, Glossogyne, Pectis*
Solanales (Order)		
	Boraginaceae	*Heliotropium*
Scrophulariales (Order)		
	Acanthaceae	*Blepharis*
	Scrophulariaceae	*Anticharis*

C_3 and C_4 appear in a single genus several times suggesting multiple independent evolution events

Family	Genus
Aizoaceae	*Mollugo*
Amaranthaceae	*Aerva, Alteranthera*
Boraginaceae	*Heliotropium*
Chenopodiaceae	*Atriplex, Bassia, Kochia, Suaeda*
Compositae	*Flaveria, Pectis*
Cyperaceae	*Cyperus, Scirpus*
Euphorbiaceae	*Chamaesyce, Euphorbia*
Gramineae	*Alloteropsis, Panicum*
Nyctaginaceae	*Boerhaavia*
Zygophyllaceae	*Kallstroemia, Zygophyllum*

Basis for ^{13}C variations in plants

There are …

irreversible steps in the metabolic process, where not all of the substrate is consumed

metabolic branch points

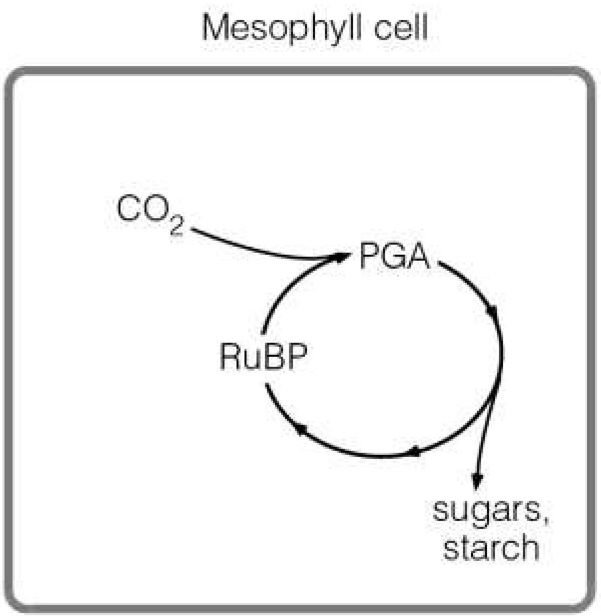
opportunities where diffusion is a fundamental step in the process

secondary fractionation events associated with common pools

Isotope effects in steps leading to CO_2 fixation in plants

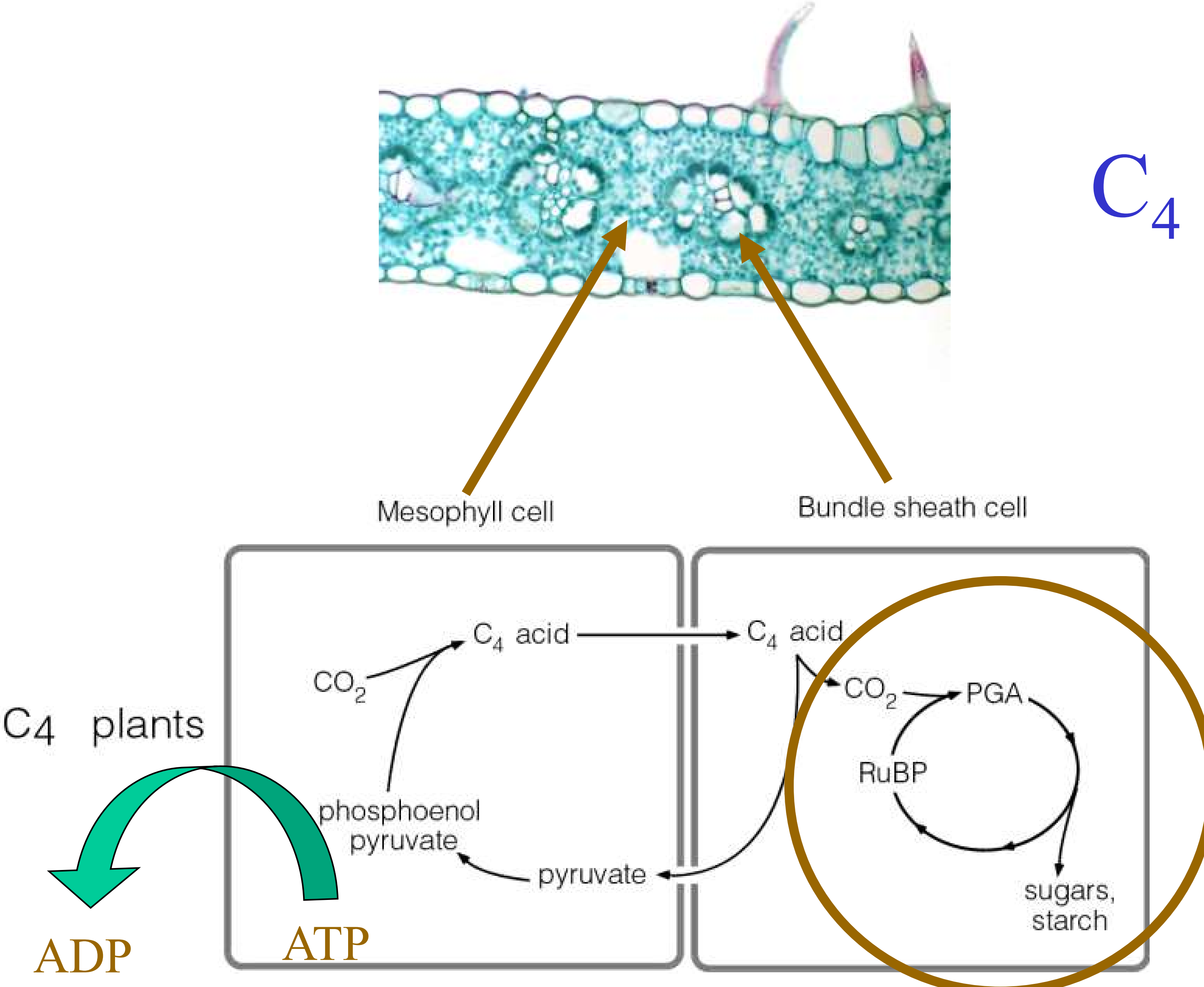
Process	Isotope Effect (α)	Discrimination (‰)	Symbol	Reference
diffusion of CO_2 in air through the stomatal pore	1.0044	4.4	a	Craig
diffusion of CO_2 in air through the boundary layer to the stomatal	1.0029	2.9	a_b	Farquhar
diffusion of dissolved CO_2 through H_2O	1.0007	0.7	a_l	O'Leary
net C3 fixation with respect to ci/ca	1.027	27	b	Farquhar and Richards
fixation of gaseous CO_2 by Rubisco from higher plants	1.030 (pH=8)	30	b_3	Roeske and O'Leary
	1.029 (pH=8.5)	29	b_3	Guy et al
fixation of HCO_3^- by PEP carboxylase	1.0020	2.0	b_4*	O'Leary et al
	1.0020	2.0		Reibach and Benedict
fixation of gaseous CO_2 (in equilibrium with HCO_3^- at 25 °C) by PEP carboxylase	0.9943	-5.7	b_4	Farquhar
equilibrium hydration of CO_2 at 25 °C	0.991	-9.0	e_b	Emrich et al
	0.991	-9.0		Mook et al
equilibrium dissolution of CO_2 into water	1.0011	1.1	e_s	Mook et al
	1.0011	1.1		O'Leary

C_3 plants



C_3

C_4



Mesophyll cell
Bundle sheath cell
C4 plants
C4 acid
CO2
phosphoenol pyruvate
pyruvate
C4 acid
CO2
PGA
RuBP
sugars, starch
ADP
ATP

RuBP carboxylase/oxygenase

$$RuBP + CO_2 \longrightarrow 2\ PGA$$

$$RuBP + O_2 \longrightarrow PGA + PG$$

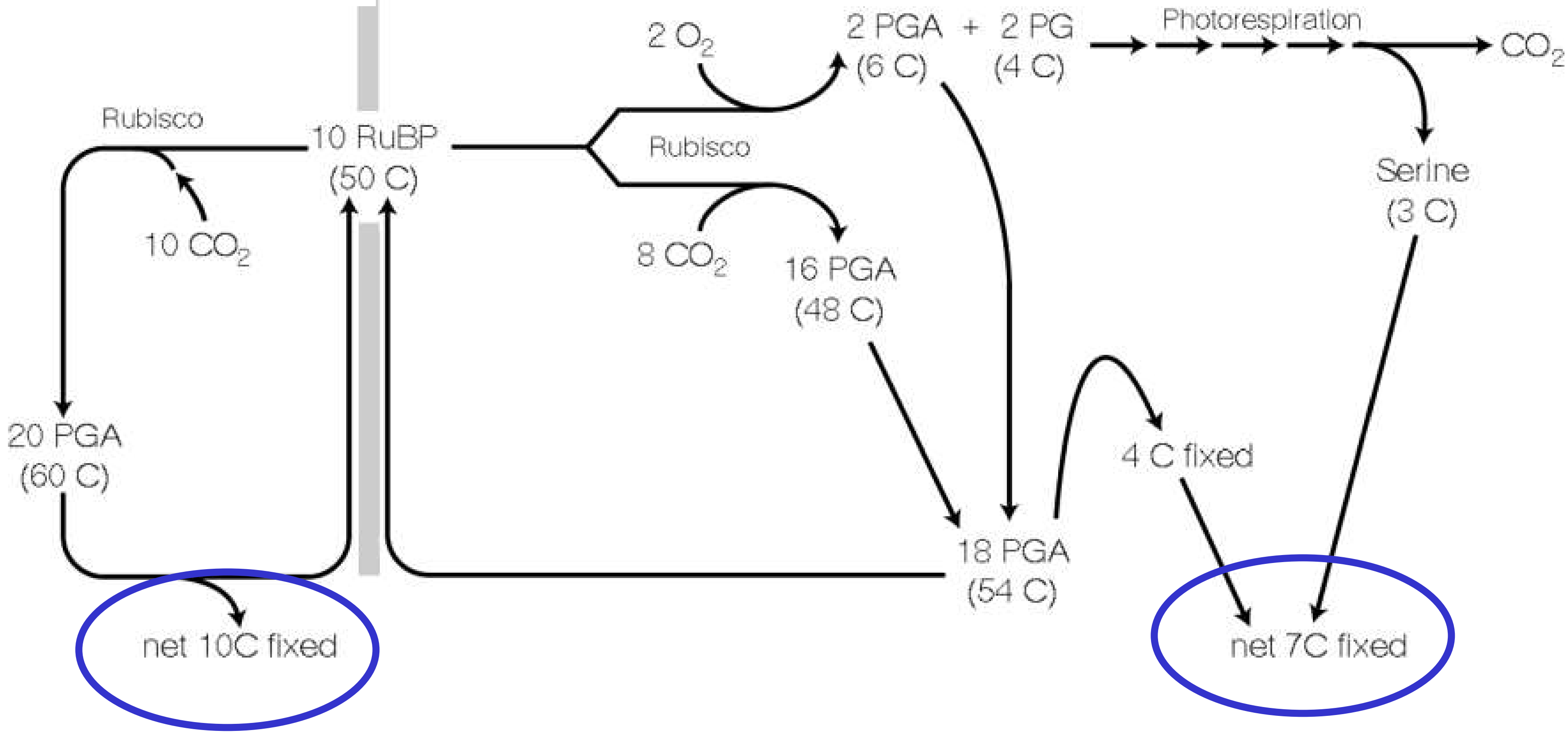
$$PG \Downarrow CO_2$$

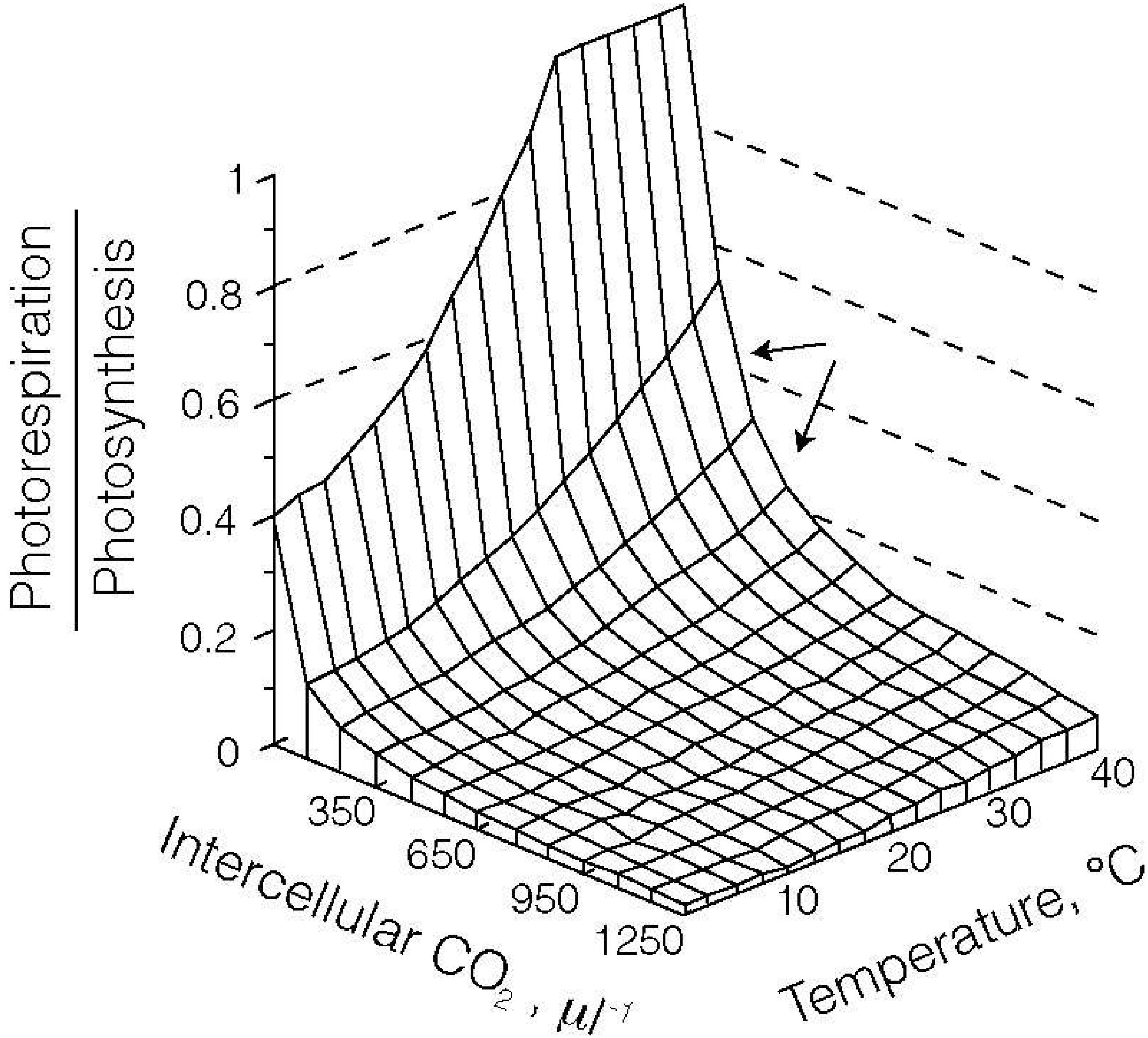
... depends on $[CO_2]$ / $[O_2]$

A change in the atmosphere will influence the PCR-PCO balance

2,000 ppm CO_2
21 % O_2

360 ppm CO_2
21 % O_2

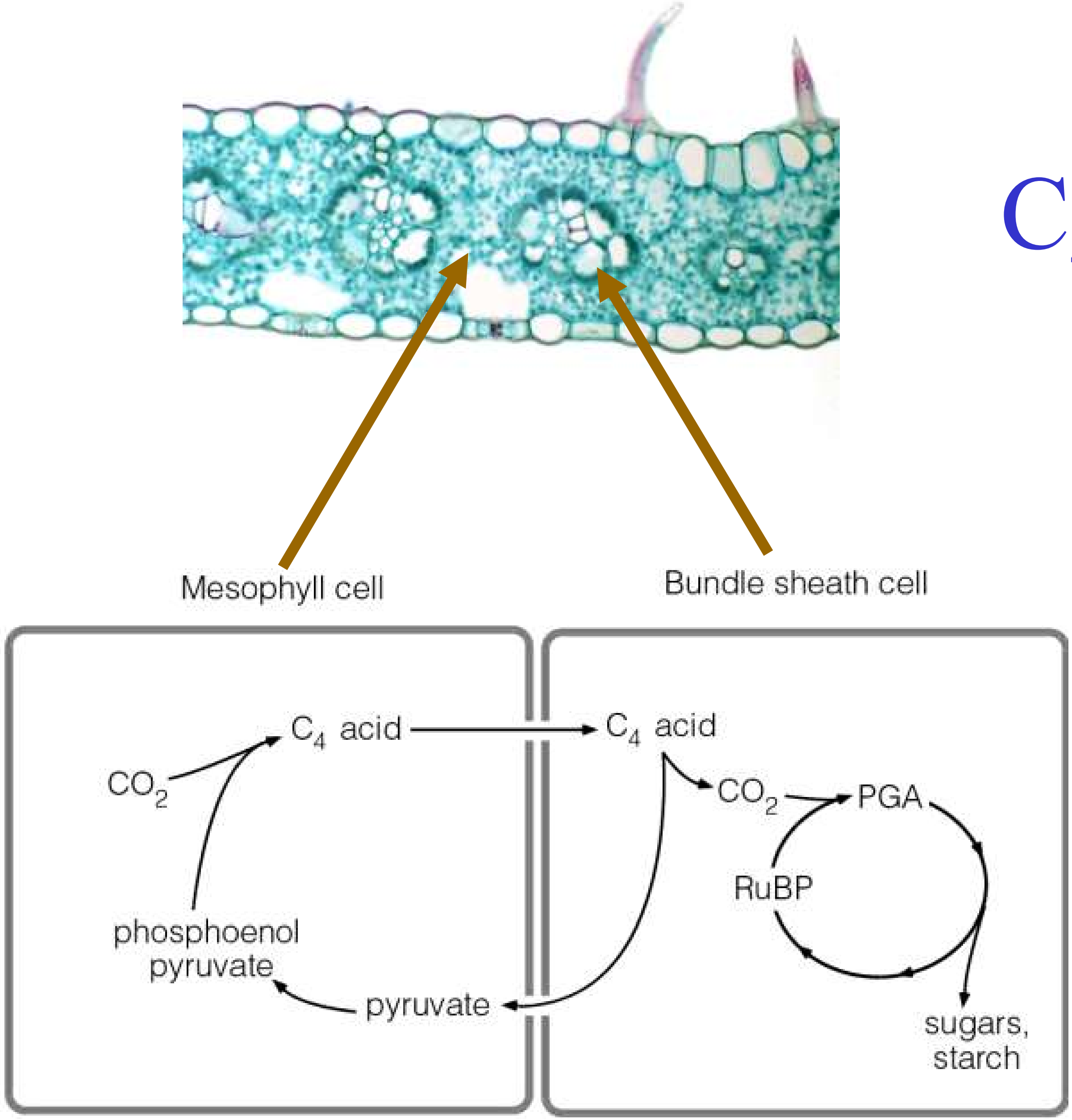




Photorespiration
Photosynthesis
1
0.8
0.6
0.4
0.2
0
350
650
950
1250
Intercellular CO_2, μl^{-1}
10
20
30
40
Temperature, °C

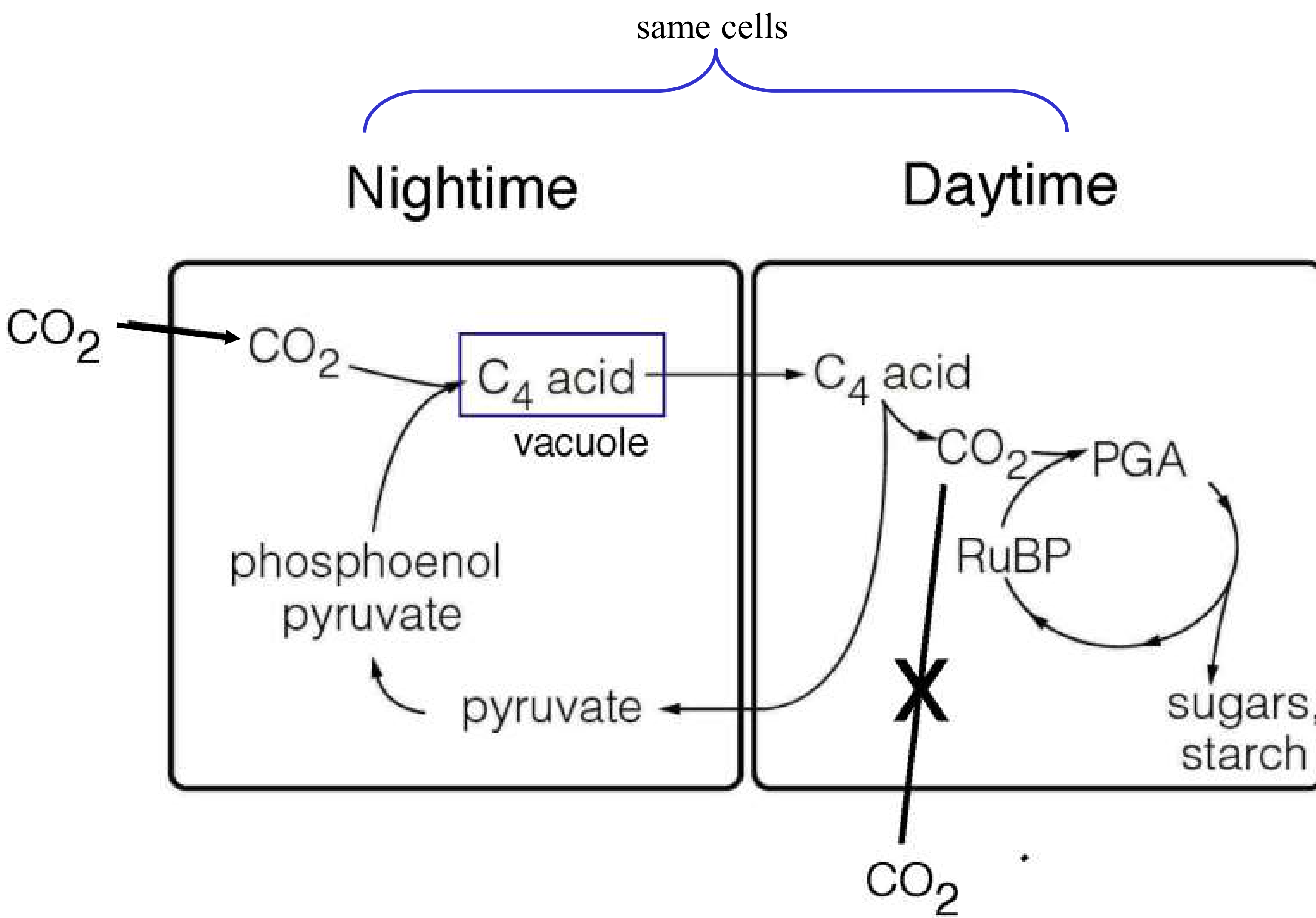
C_4

C_4 plants


Mesophyll cell
Bundle sheath cell
C4 acid
CO2
phosphoenol pyruvate
pyruvate
C4 acid
CO2
PGA
RuBP
sugars, starch

CAM plants

How the CAM cycle differs from C_4 photosynthesis



stomates open at night

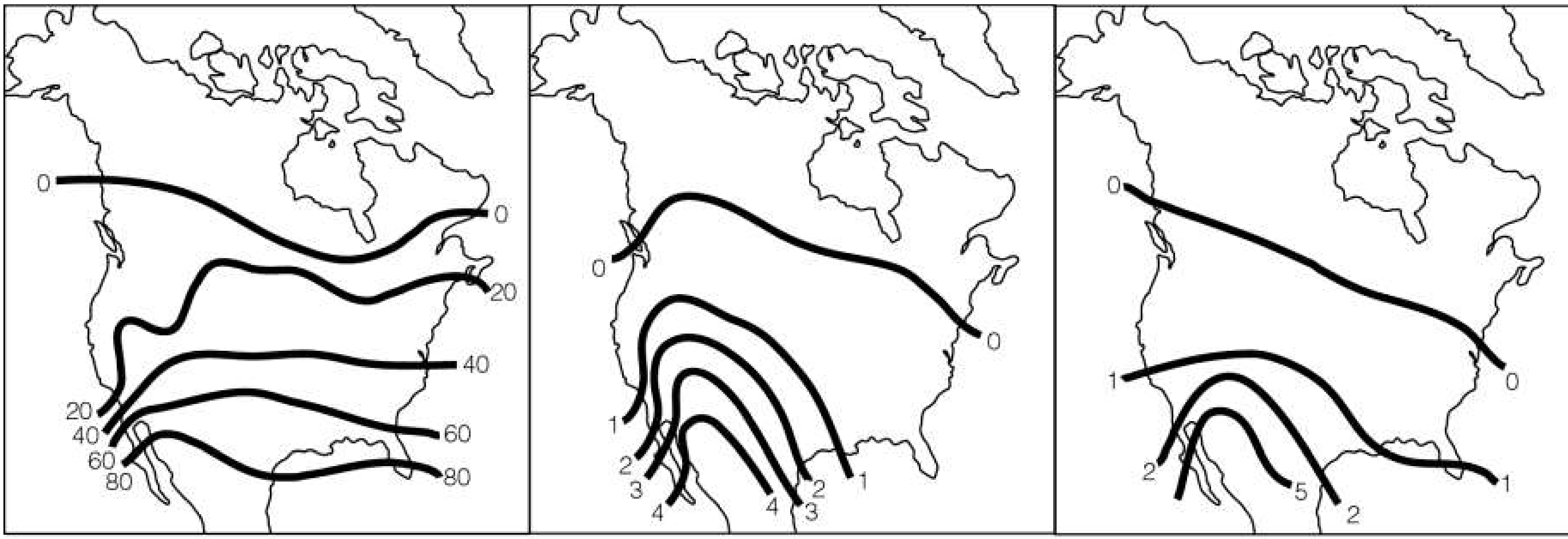
stomates closed during day

CAM present in ferns, gymnosperms, and angiosperms

independent evolution probably also occurred

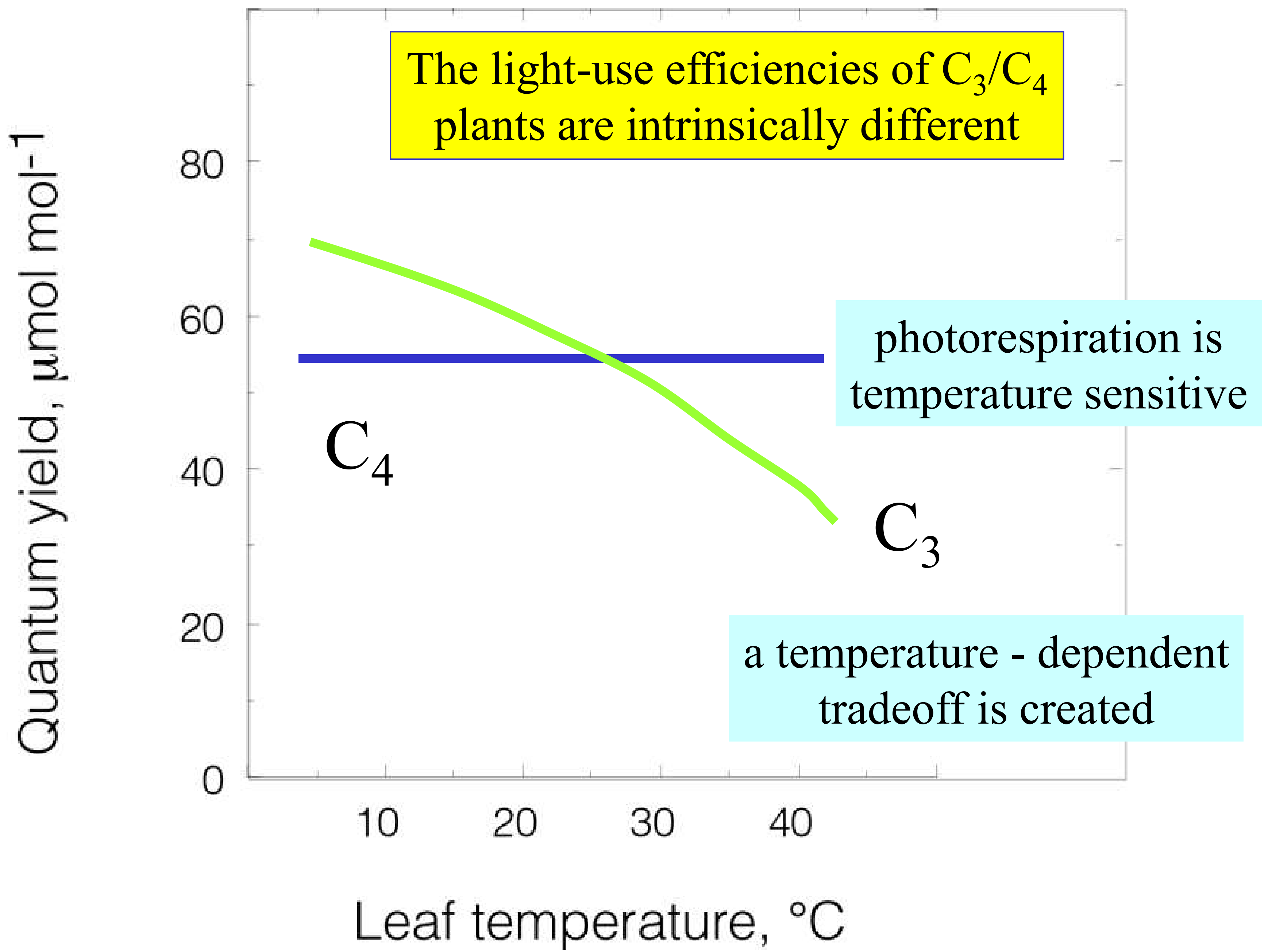
Polypodiales	Polypodiaceae
Gymnospermae	Welwitschiaceae
Monocotyledonae	Agavaceae, Bromeliaceae, Liliaceae, Orchidaceae
Dicotyledonae	Aizoaceae, Asclepiadaceae, Bataceae, Cactaceae, Capparidaceae, Caryophyllaceae, Chenopodiaceae, Compositae, Crassulaceae, Cucurbitaceae, Didiereaceae, Euphorbiaceae, Geraniaceae, Labiatae, Oxalidaceae, Passifloraceae, Piperaceae, Plantaginaceae, Portulacaceae, Tetragoniaceae, Vitaceae

The abundance of C_3/C_4 plants varies along environmental gradients

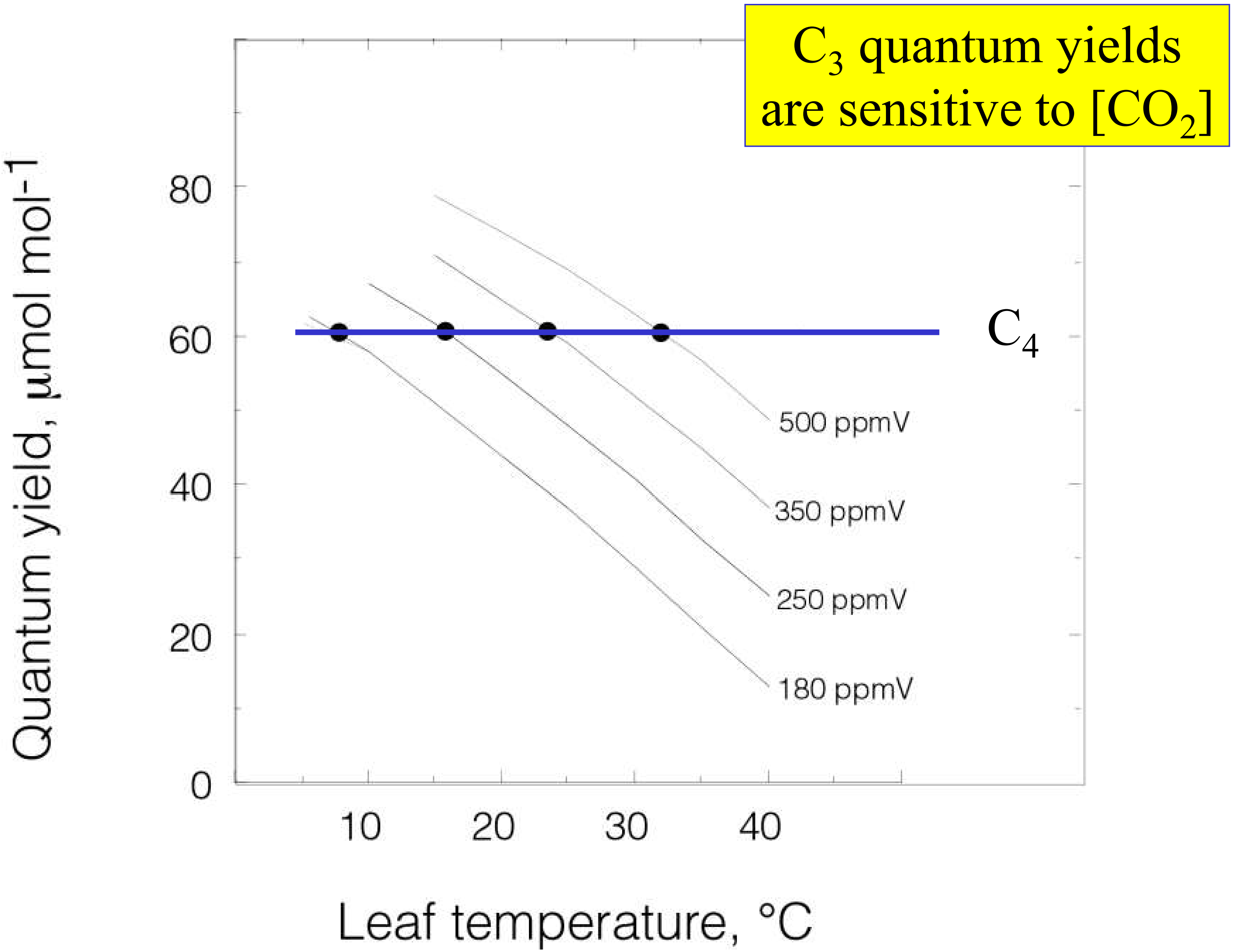


C_4 Grasses　　C_4 Dicots　　CAM

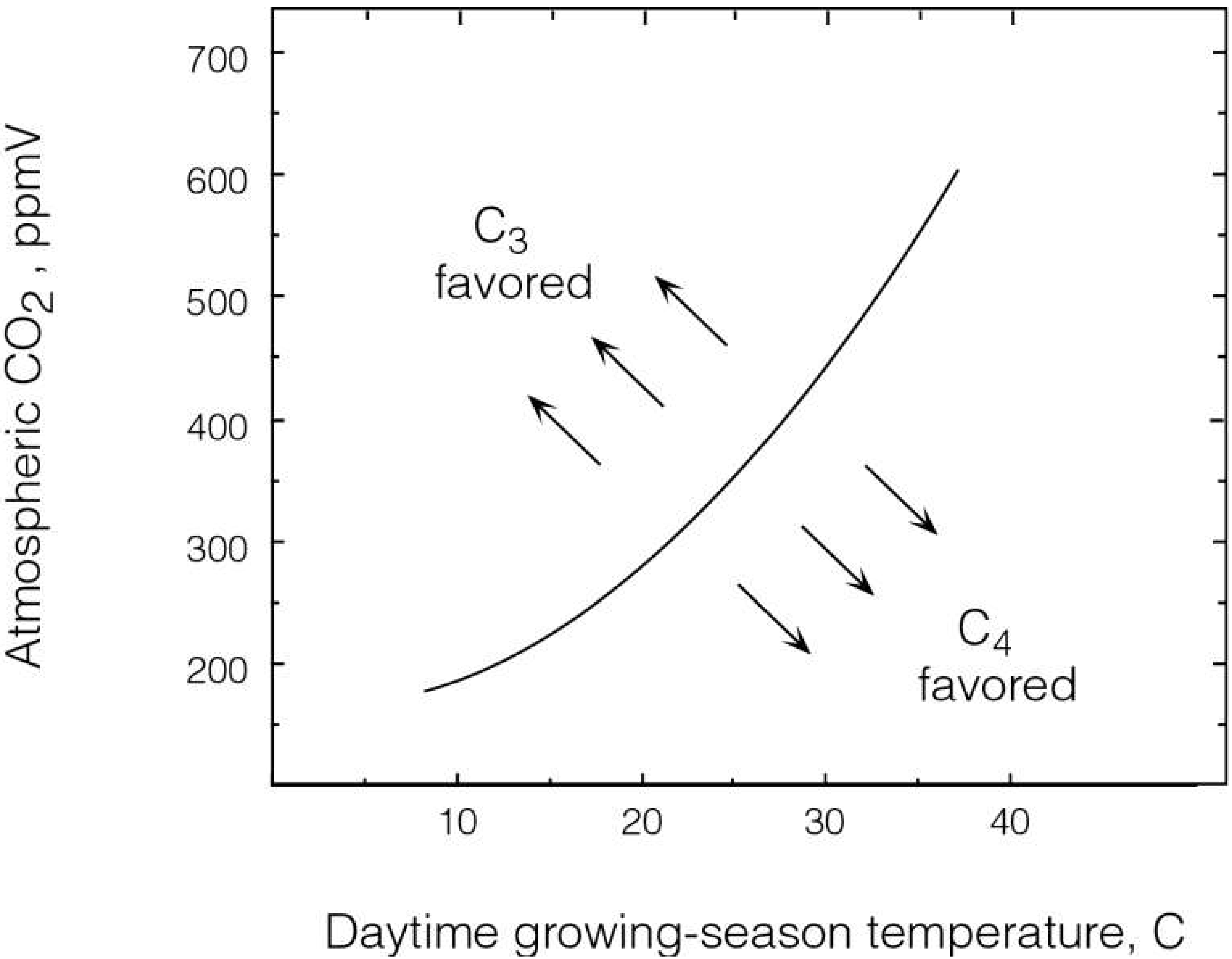
Ehleringer (1979)



The light-use efficiencies of C3/C4 plants are intrinsically different
photorespiration is temperature sensitive
a temperature - dependent tradeoff is created
C4
C3
Quantum yield, µmol mol-1
80
60
40
20
0
10
20
30
40
Leaf temperature, °C

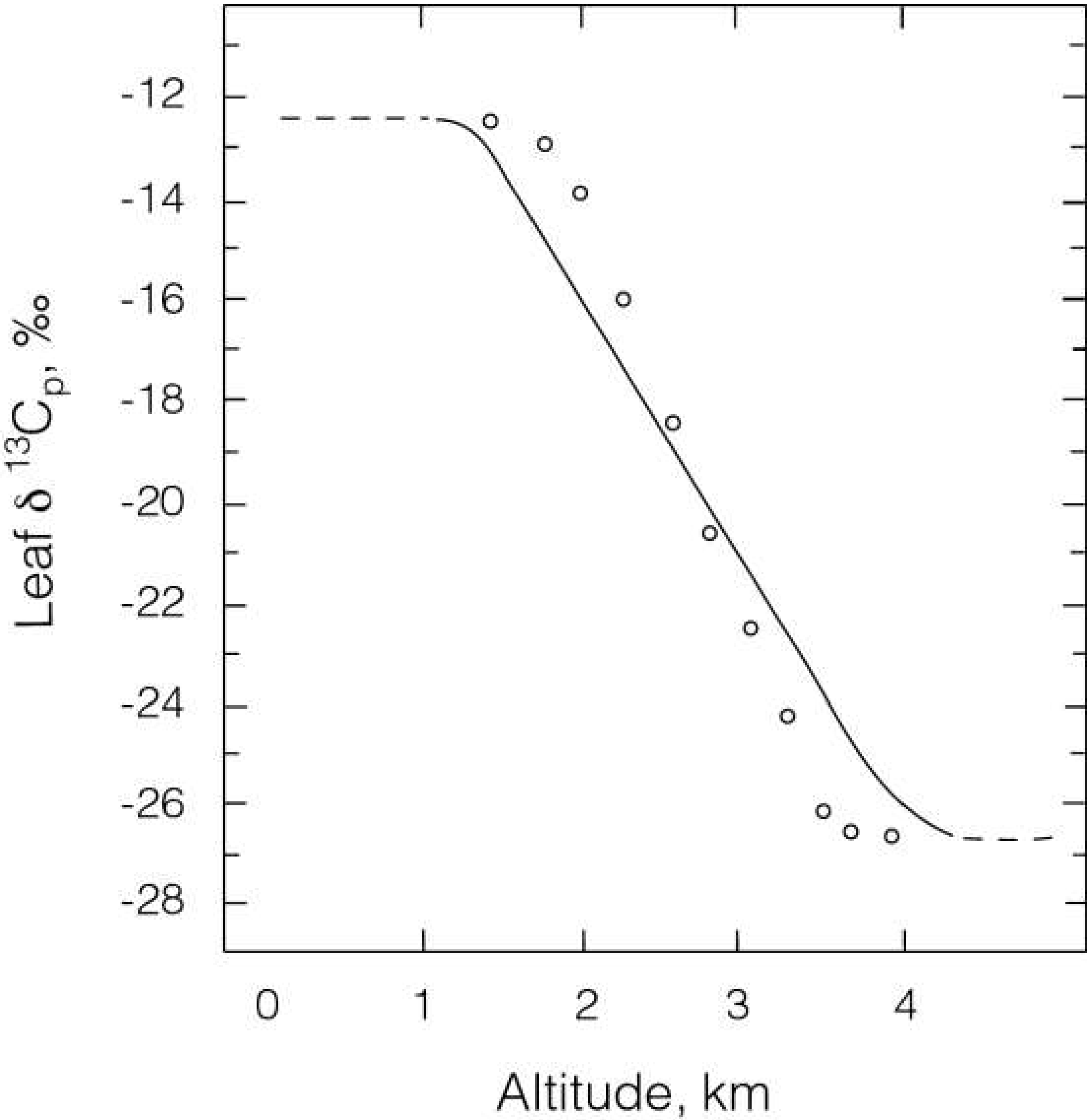

C3 quantum yields are sensitive to [CO2]
C4
Quantum yield, µmol mol-1
80
60
40
20
0
10
20
30
40
500 ppmV
350 ppmV
250 ppmV
180 ppmV
Leaf temperature, °C

The distribution of C_3/C_4 plants relates to CO_2 and temperature



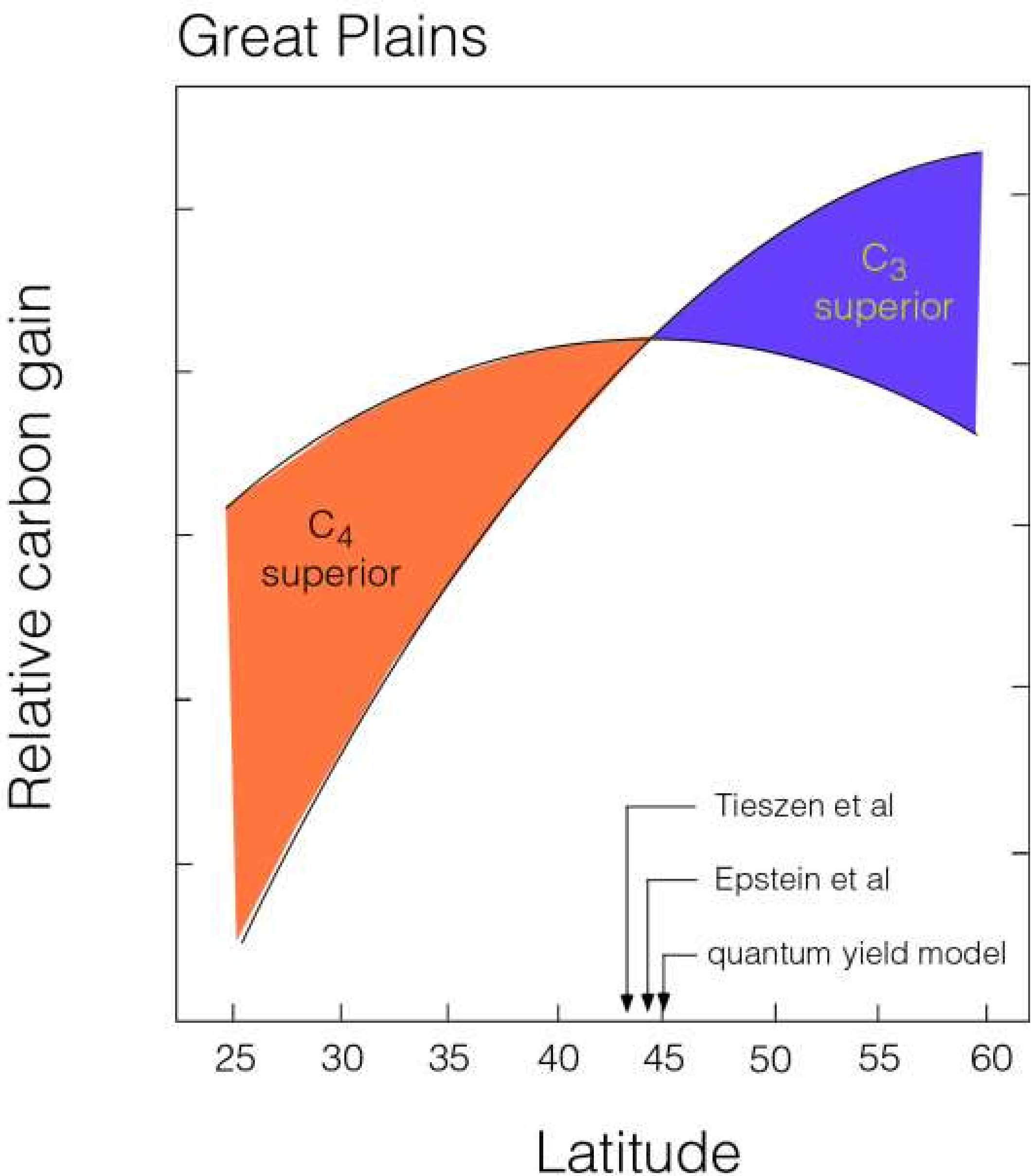
Ehleringer et al (1997)

The abundance of C_3/C_4 plants varies along environmental gradients



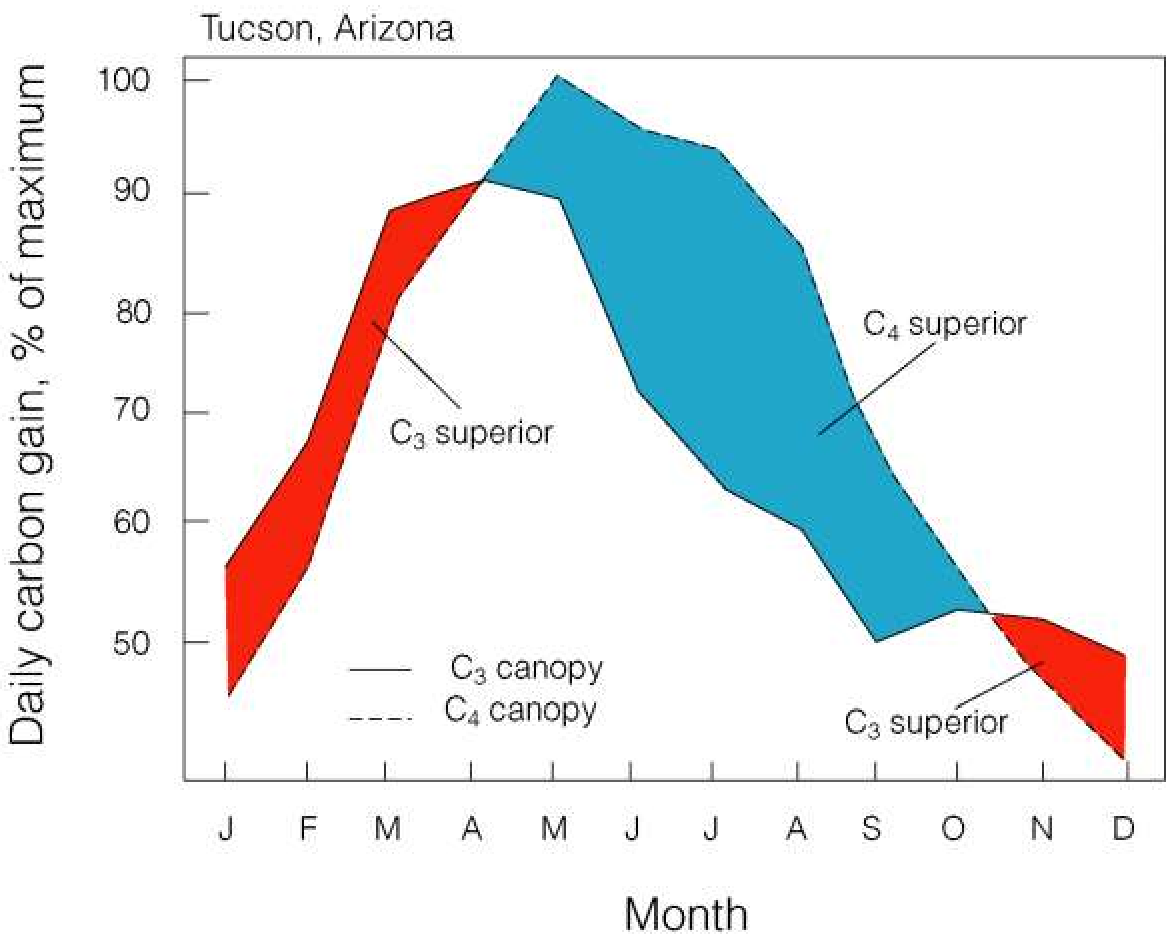
Tieszen et al (1979)

C_4 abundance is predicted to decrease with increasing latitude



Ehleringer (1978)

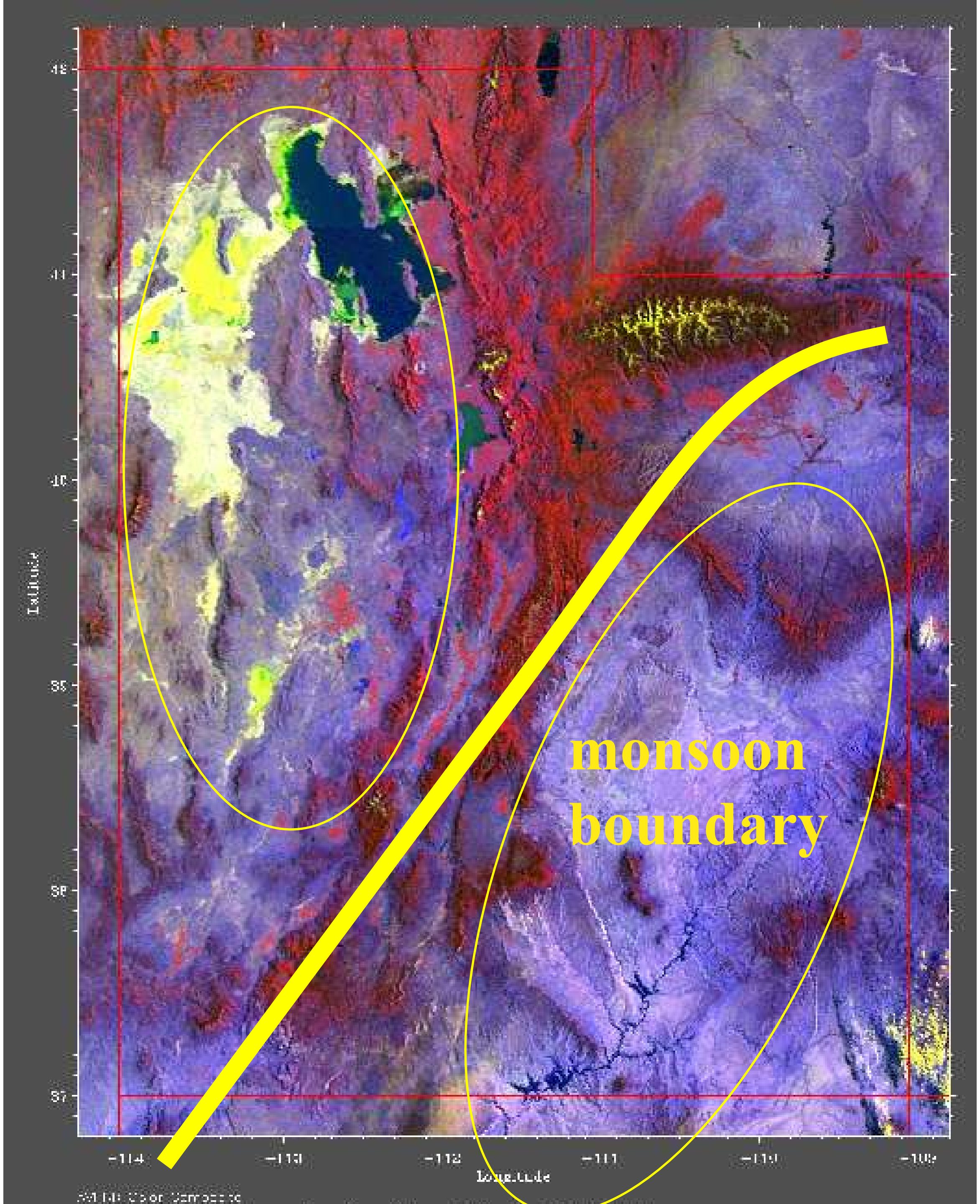
C_4 abundance is predicted to decrease in cool growing seasons



Ehleringer (1978)

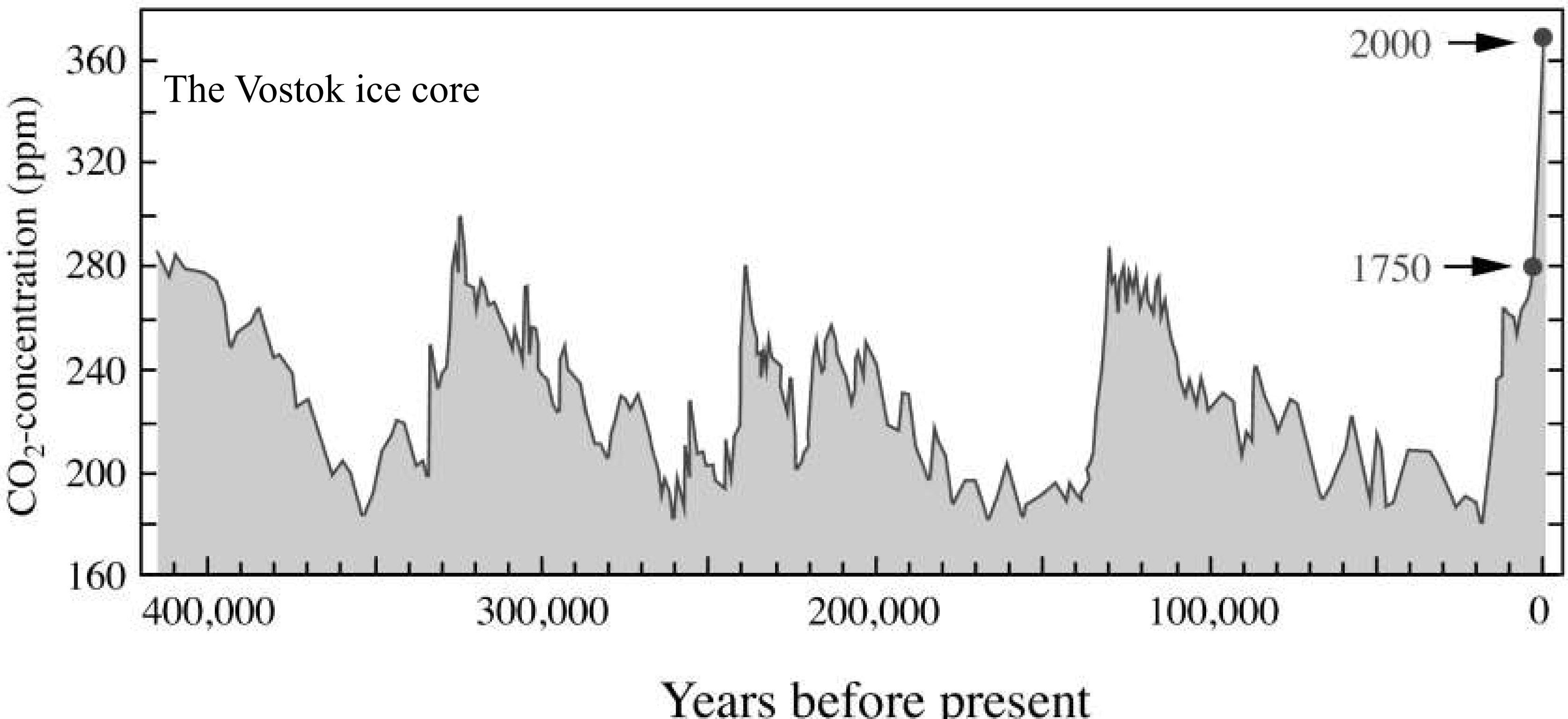
Utah

C_4:
halophyte shrubs

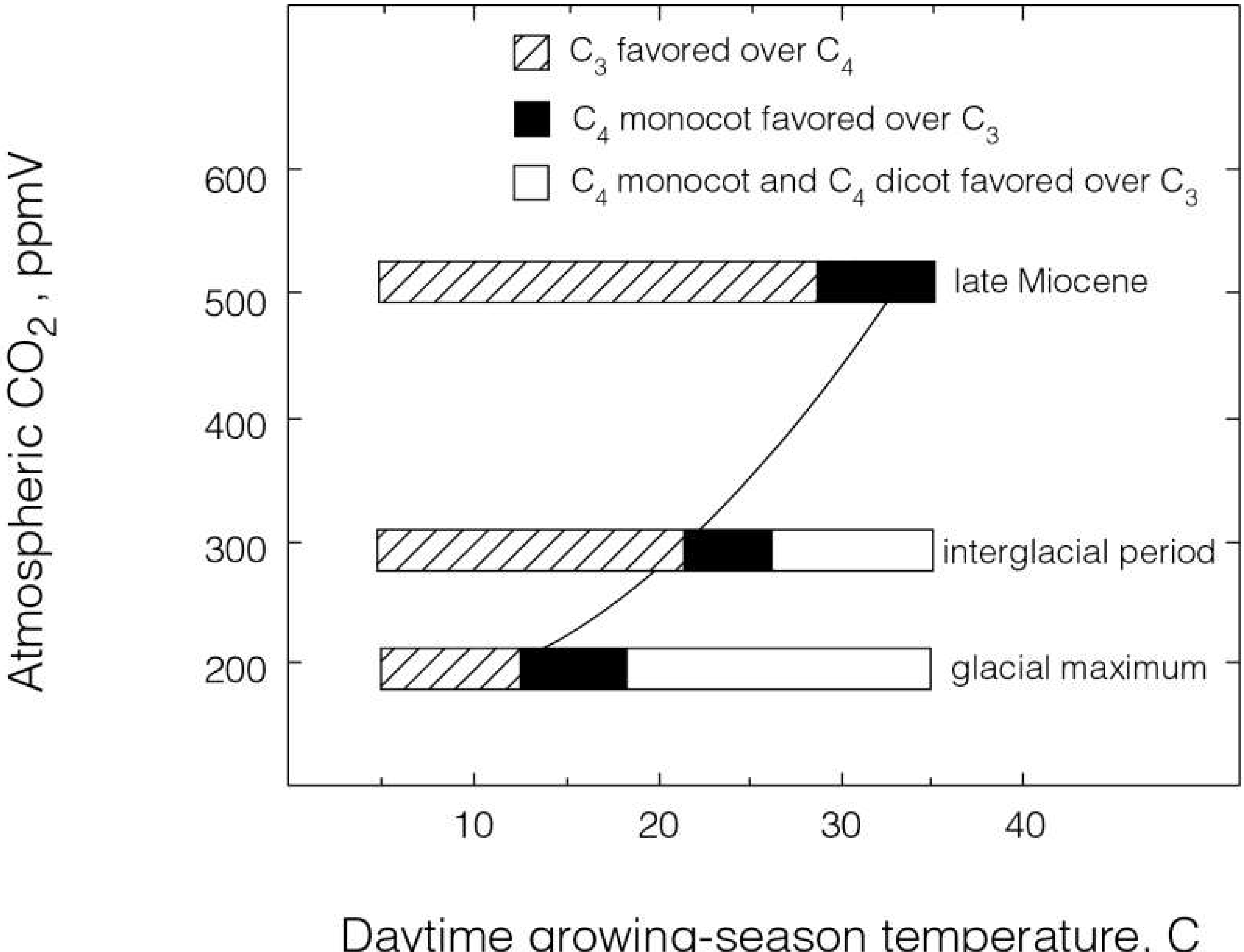


C_4:
halophyte shrubs
grasses
annuals

What climate drivers are important for photosynthesis
Relationships between C_3/C_4 photosynthesis and climate

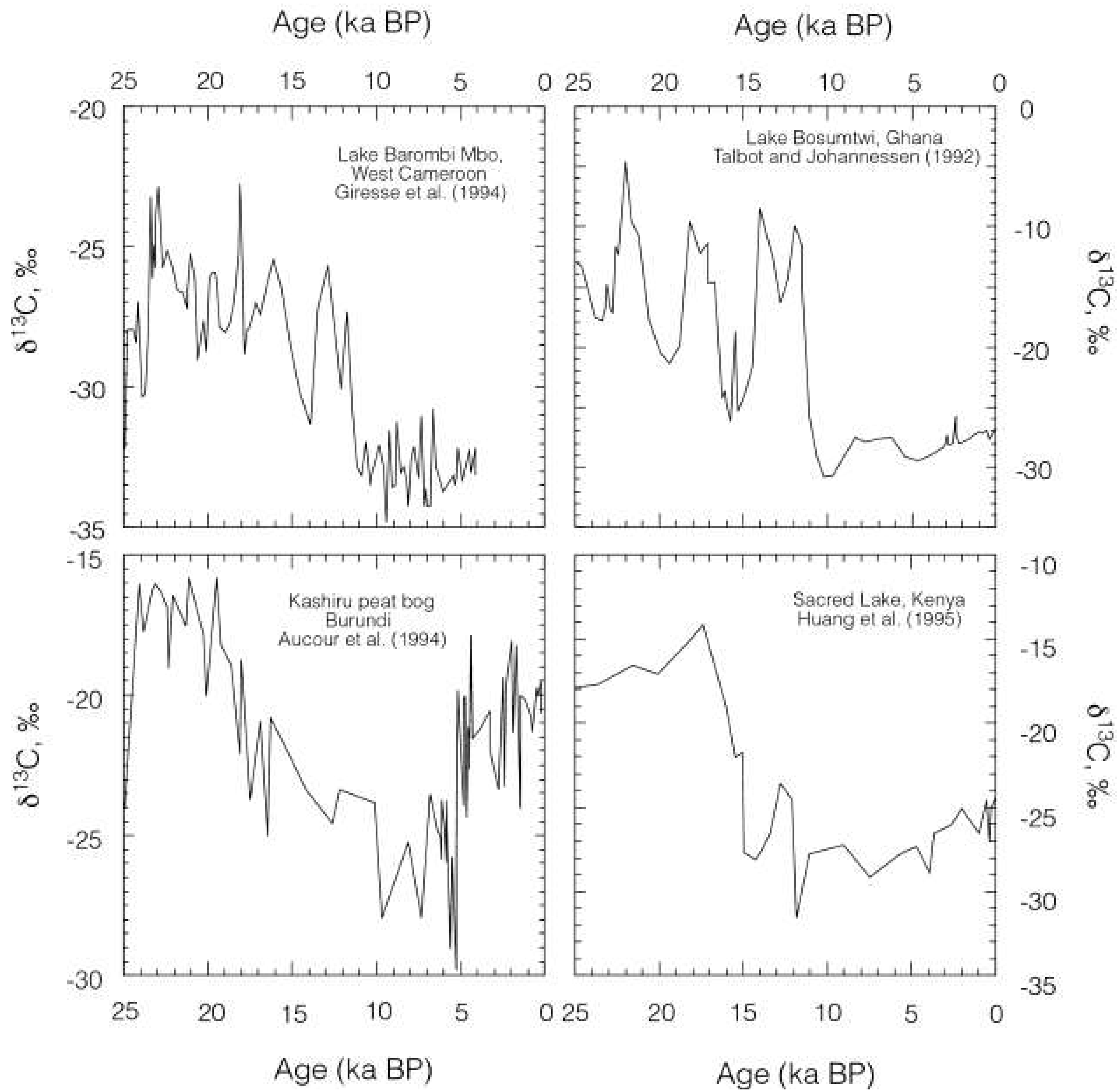


C_4 plant distributions are predicted to expand as CO_2 decreases



Ehleringer et al (1997)

C_4 plant distributions apparently increased as CO_2 decreased

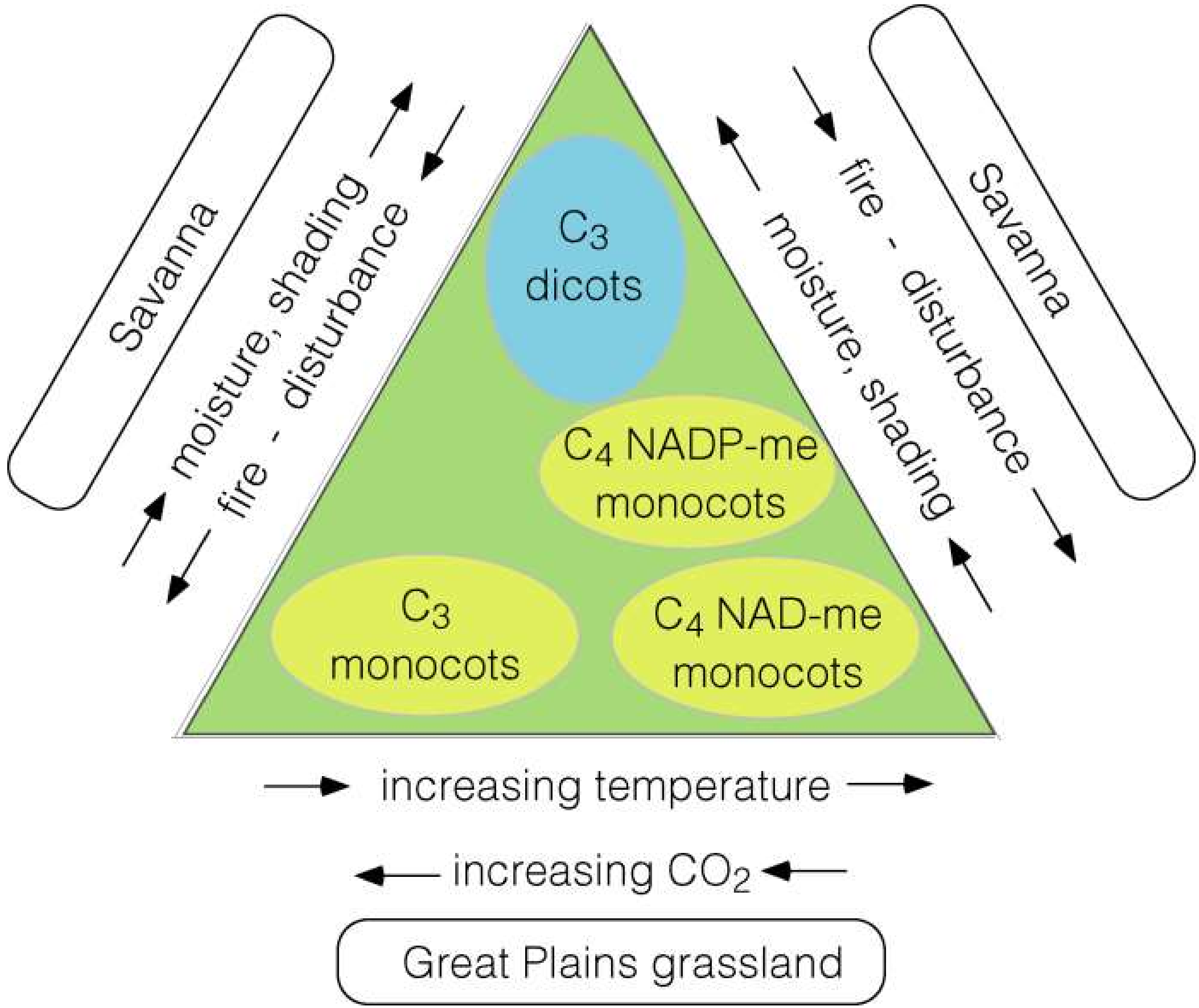


Ehleringer et al (1997)

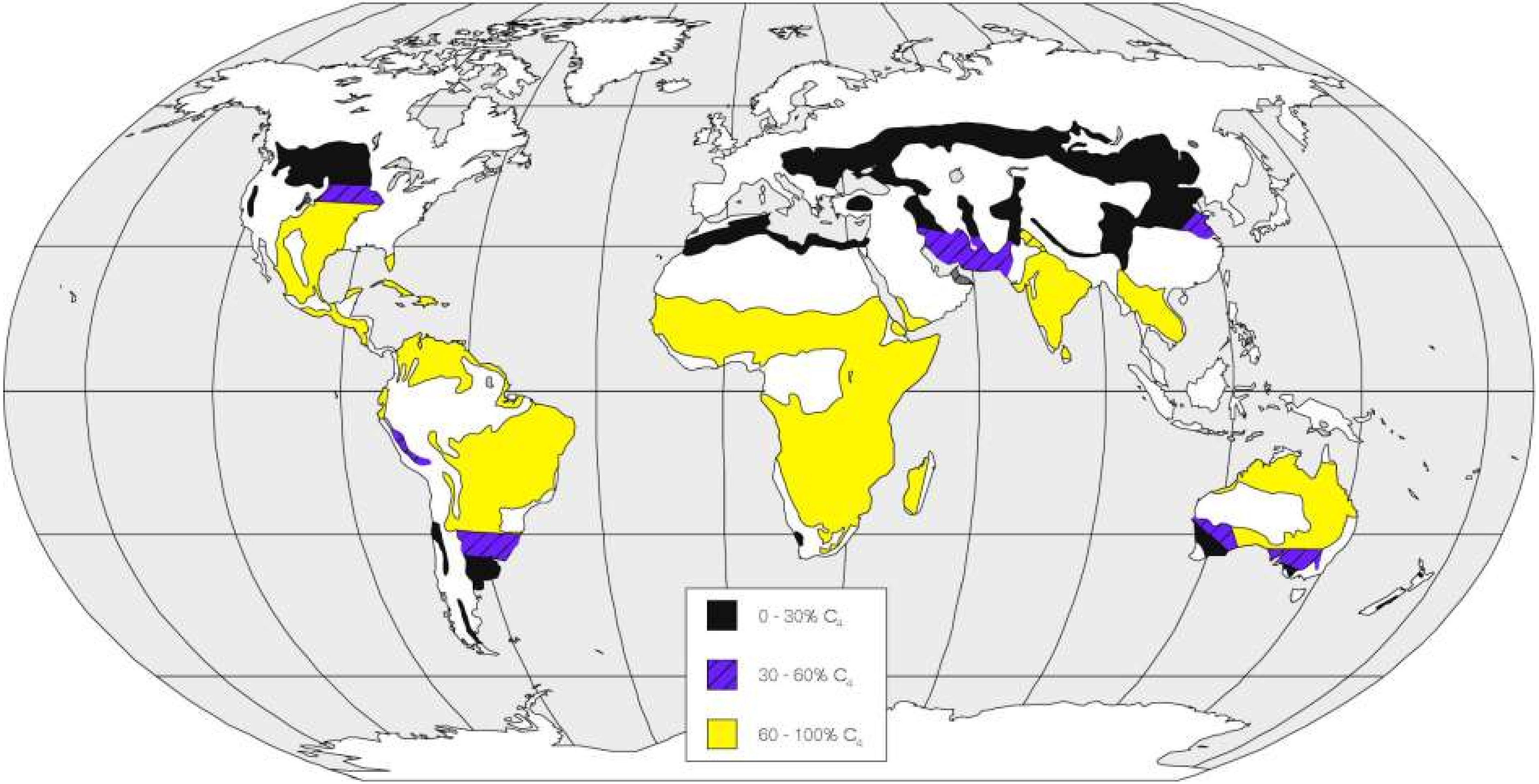

(Niger) Niamey
Ouagadougou
aso
N'Djamena (N'Djamena)
Benin
Abuja
Nigeria
Togo
a
(Porto Novo)
Lagos
Lake Baleng
Mahin Canyon
Lake Manenguba
Lomé
Kamerun
Lake Barombi Mbo
Lake Ossa
Bangui
Lake Ossa, Kamerun
(Jaunde)
Golf von Guinea
Äquatorialguinea
São Tomé
Libreville
Kongo
Gabun
Demokratis


Kumbo
Bamenda
N 11
N6
Lake Baleng
Dschang
Bafoussam
Foumbot
Kamerun
Bafang
Lake Manenguba
Bangangté
Nkongsamba
N4
Bafia
Lake Barombi Mbo
N 16
N 15
N8
unsha lake
N 5
N 1
Douala
N10
Lake Ossa
(Jaunde)
labo
Lake Ossa, Kamerun
N2
N 7
Image © 2009 TerraMetrics
US Dept of State Geographer
© 2009 Google
© 2009 Europa Technologies
Google
Mbalmayo
s Nguema
4°52'14.05" N 10°31'08.03" E
Höhe 635 m
Sichthöhe 358.59 km

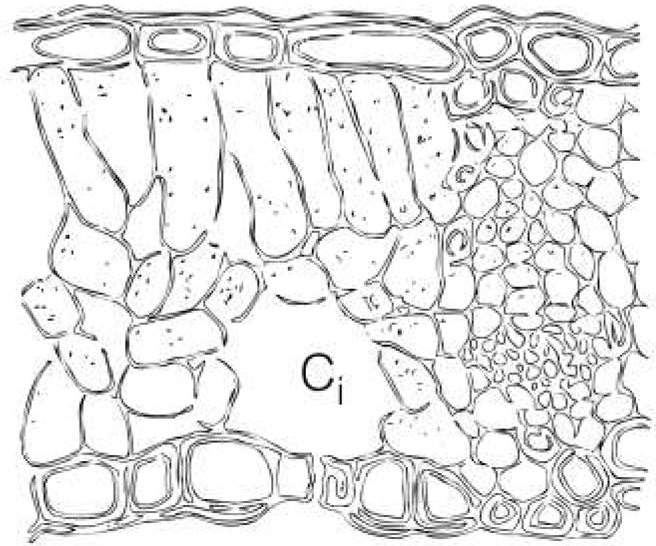
C_4 subtype and disturbance are also factors to consider



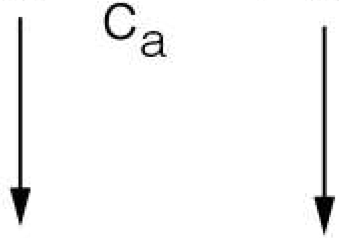
Distributions of C_3 and C_4 grasses in the savanna and steppe ecosystems



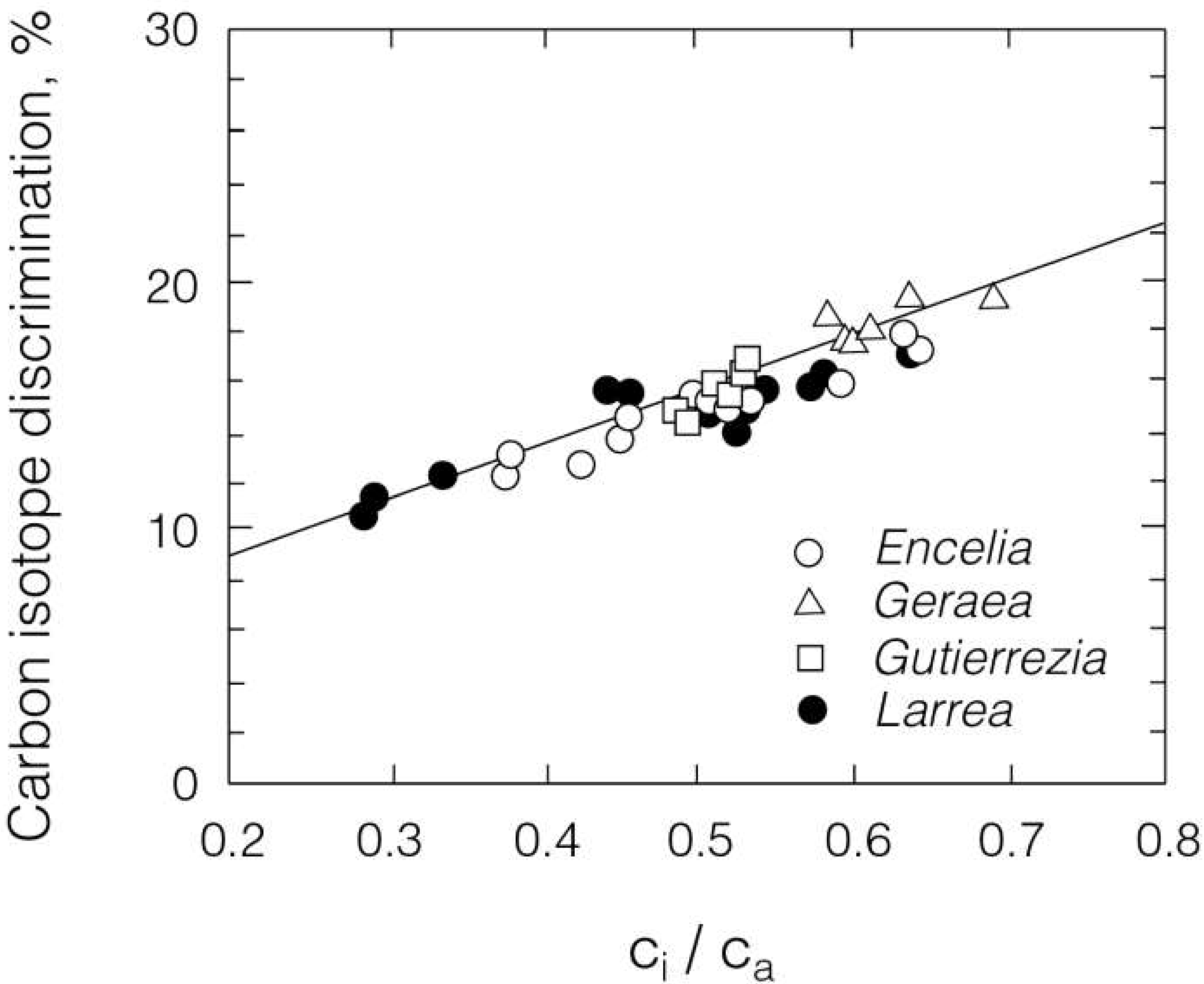
Carbon isotope discrimination in C_3 plants



$$\Delta = a\frac{c_a - c_i}{c_a} + b\frac{c_i}{c_a} = a + (b - a)\frac{c_i}{c_a}$$



C_3 carbon isotope discrimination follows predicted relationship



Ehleringer et al (1992)

Carbon isotope discrimination in C_4 plants

$$b_4 = e_s + e_b + b_4^*$$

$$\Delta = a\frac{c_a - c_i}{c_a} + (b_4 + b_3\phi - a)\frac{c_i}{c_a} = a + (b_4 + b_3\phi - a)\frac{c_i}{c_a}$$

Process	Isotope Effect (α)	Discrimination (‰)	Symbol
fixation of gaseous CO_2 (in equilibrium with HCO_3^- at 25 ° C) by PEP carboxylase	0.9943	-5.7	b_4
equilibrium dissolution of CO_2 into water	1.0011	1.1	e_s
equilibrium hydration of CO_2 at 25 ° C	0.991	-9.0	e_b
fixation of HCO_3^- by PEP carboxylase	1.0020	2.0	b_4^*

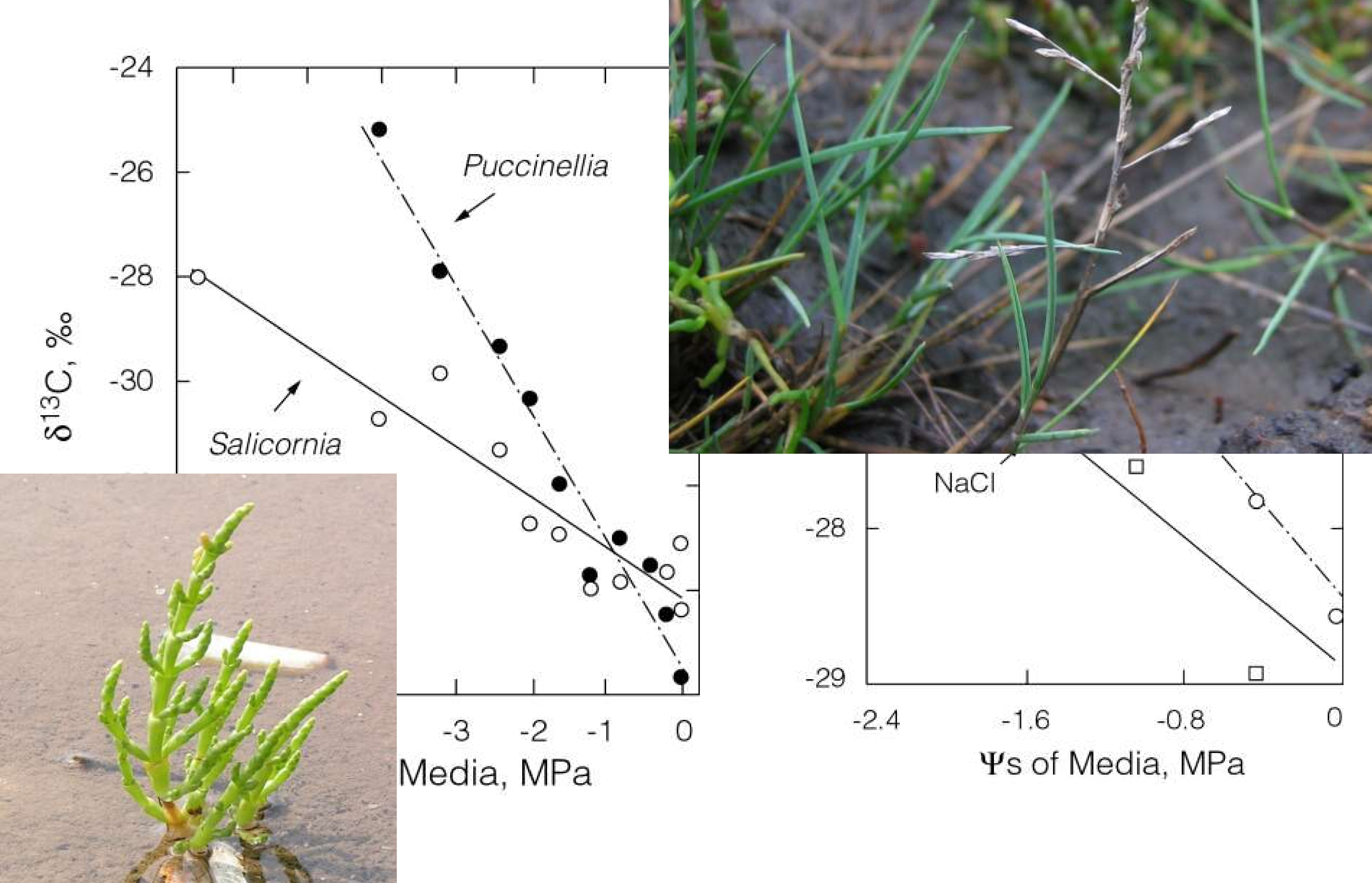
Carbon isotope discrimination in CAM plants

$$\Delta = a + (b_4 - a)\frac{c_i}{c_a}$$

Carbon isotope discrimination in aquatic C_3 plants

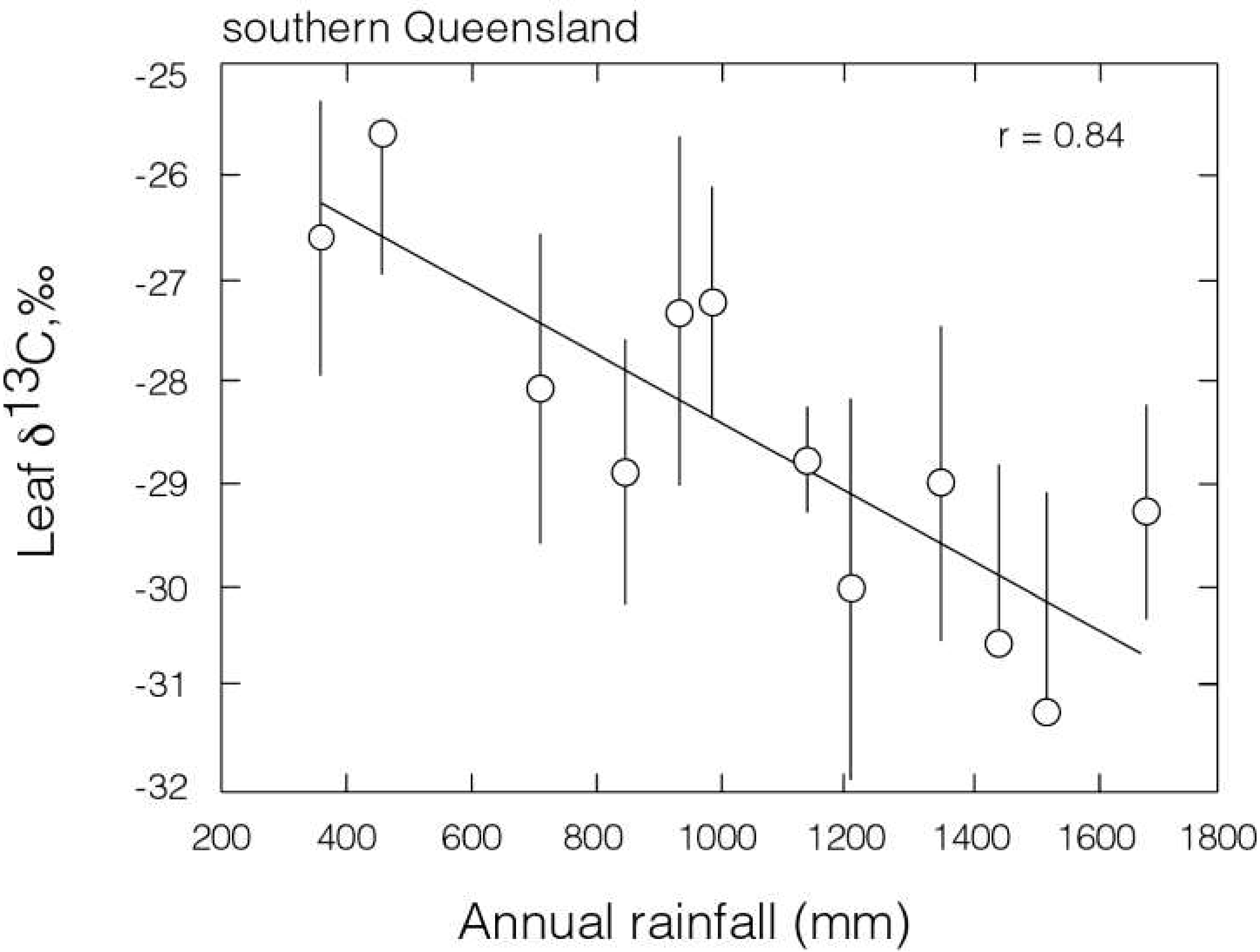
$$\Delta = (e_s + a_l)\frac{c_a - c_c}{c_a} + b_3\frac{c_c}{c_a} = e_s + a_l + (b_3 - e_s - a_l)\frac{c_c}{c_a}$$

C_3 plants discriminate less when e



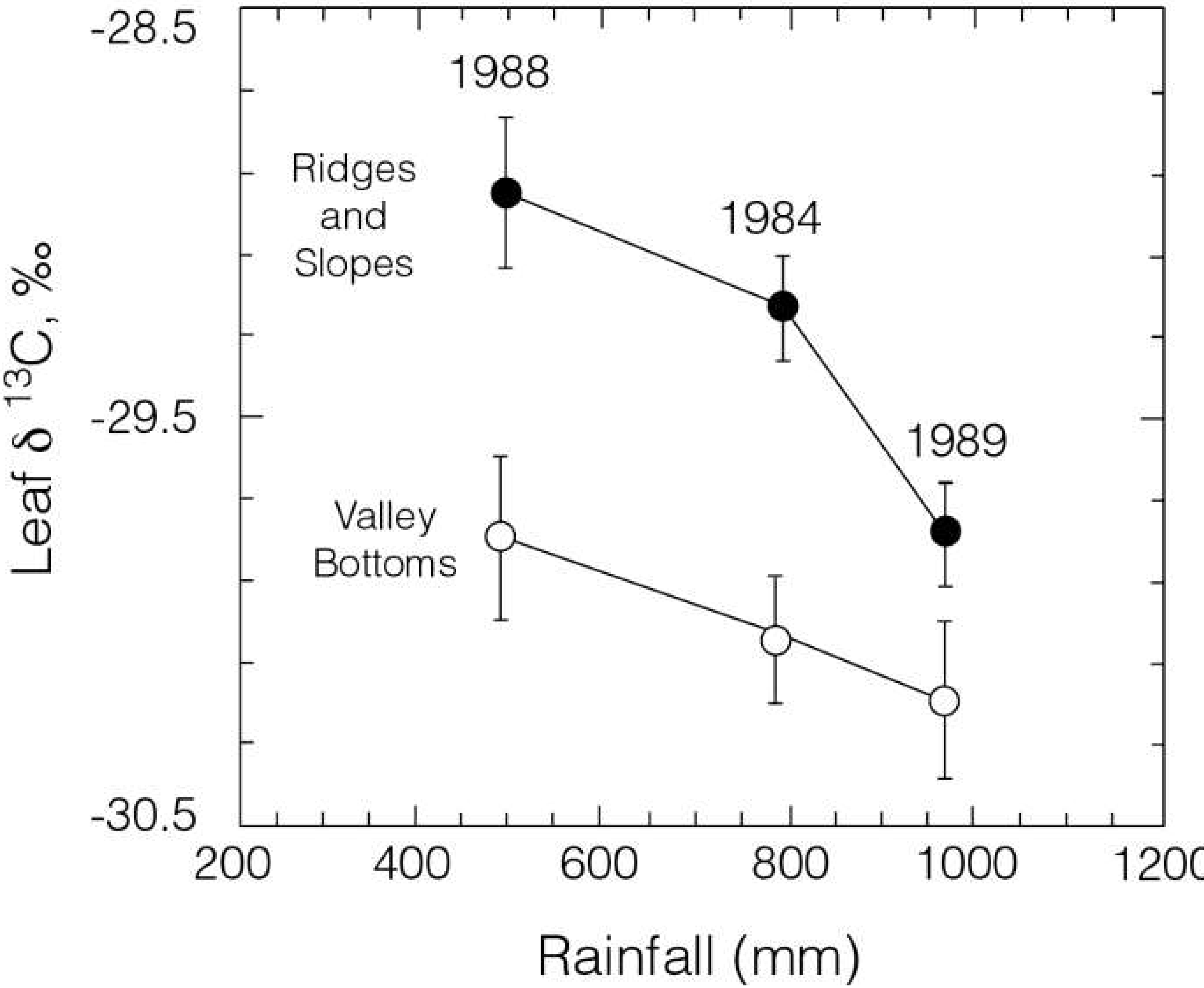
Guy et al. (1980)

We observe a decrease in C_3 discrimination along precipitation gradients



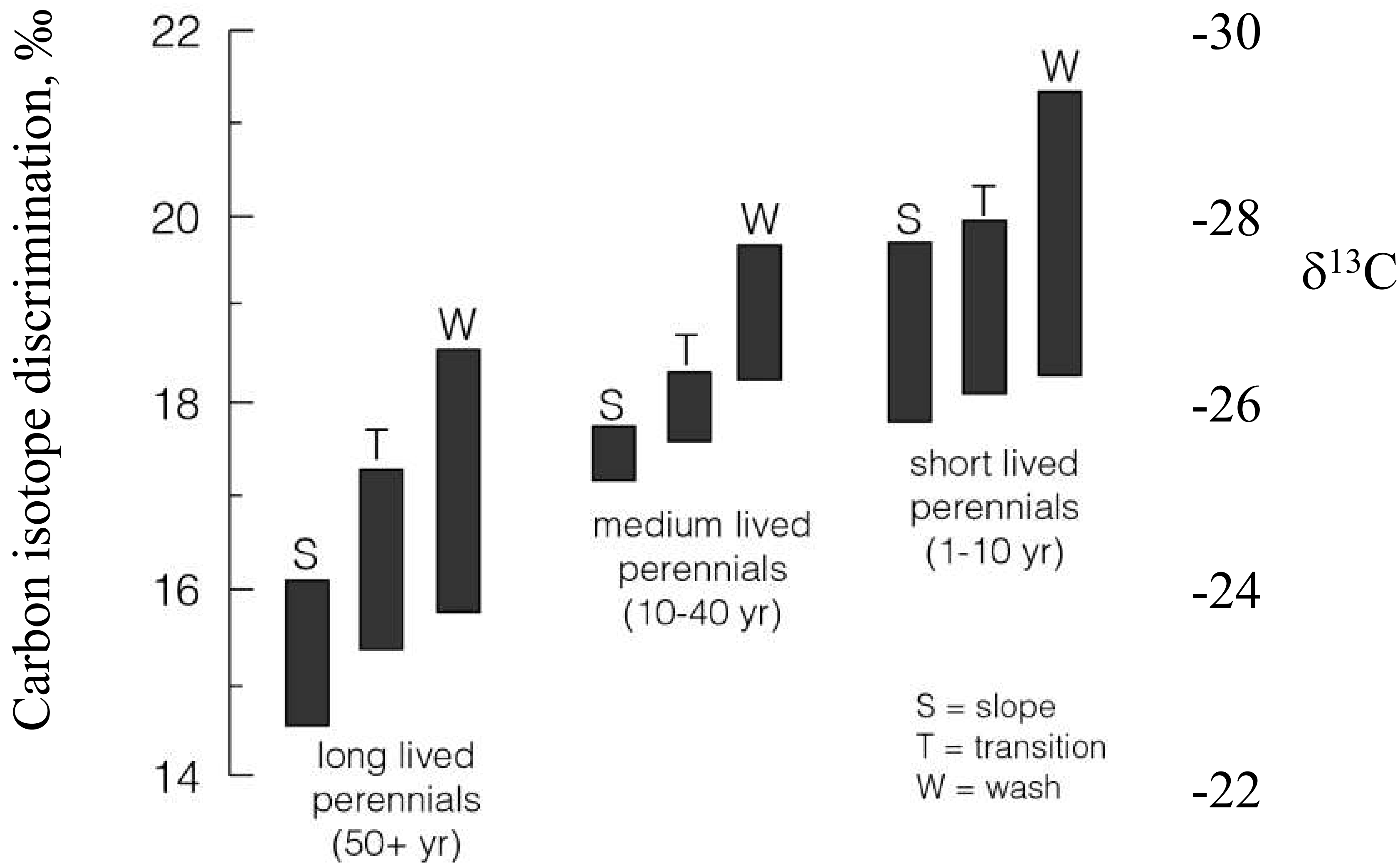
Stewart et al. (1995)

There is an adjustment response to current growth environment, but rankings among plants remain fixed.



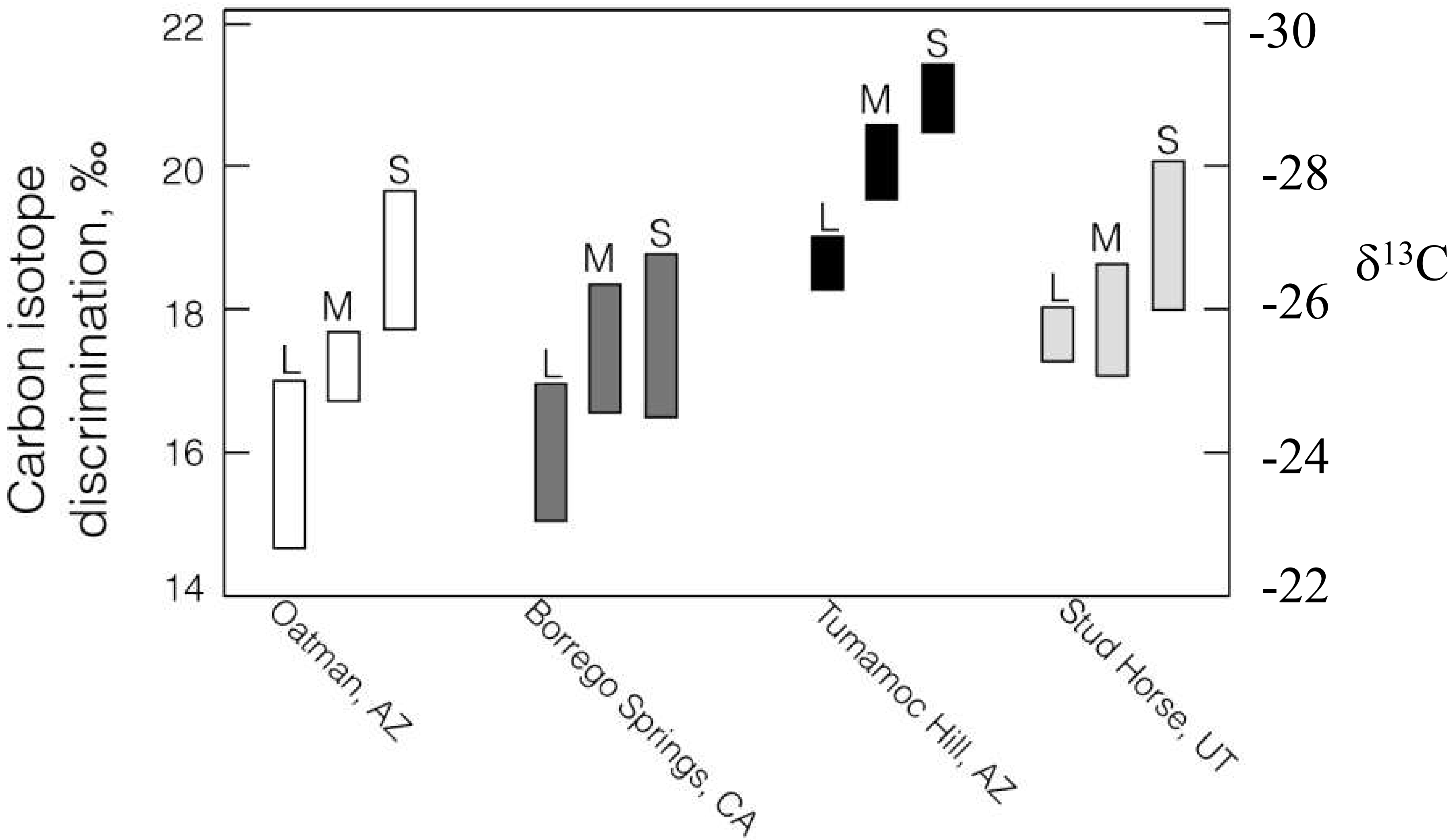
Garten and Taylor (1992)

Carbon isotope discrimination decreases with increased aridity

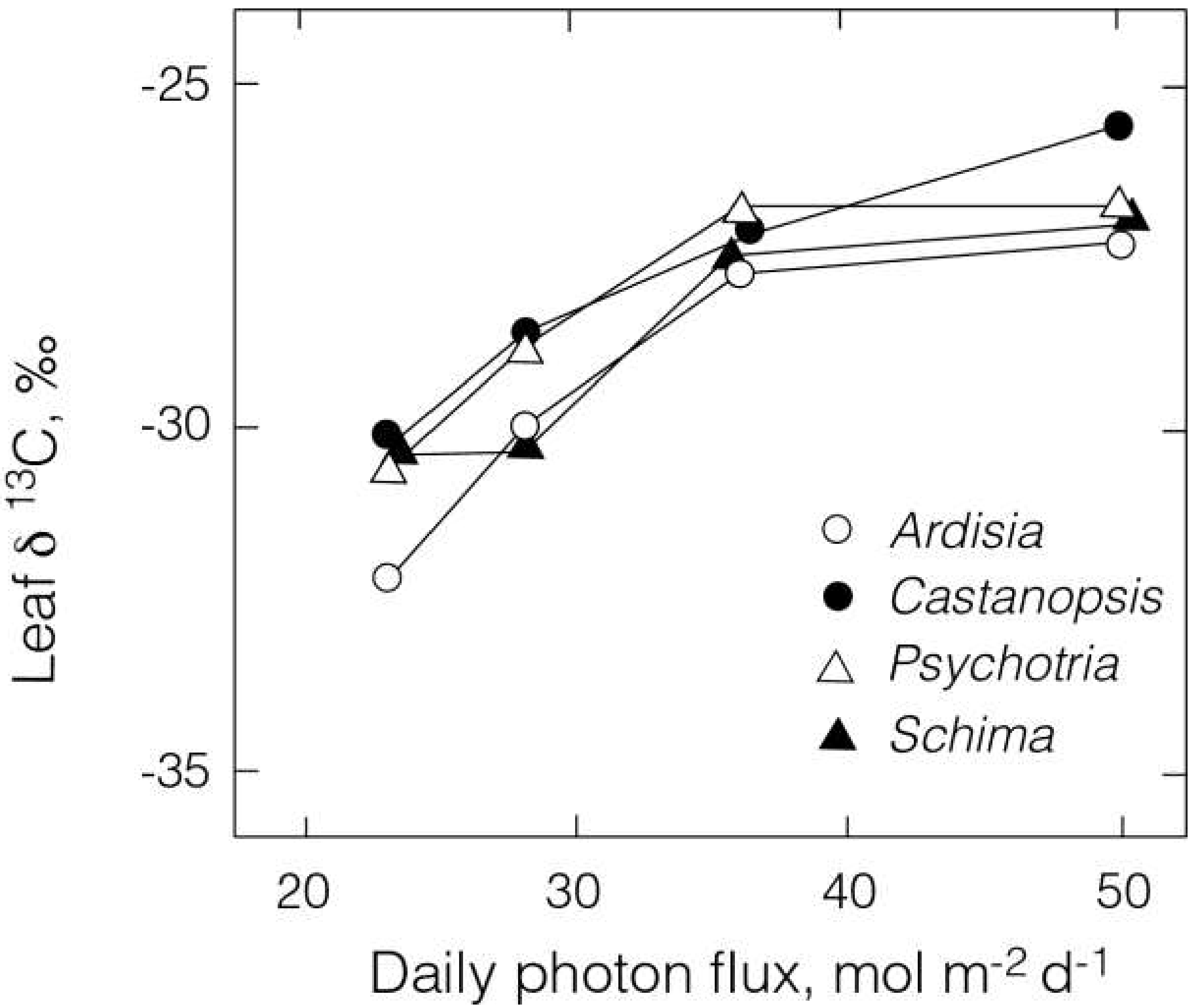


Ehleringer and Cooper (1986)

The pattern is repeated across a number of desert sites.

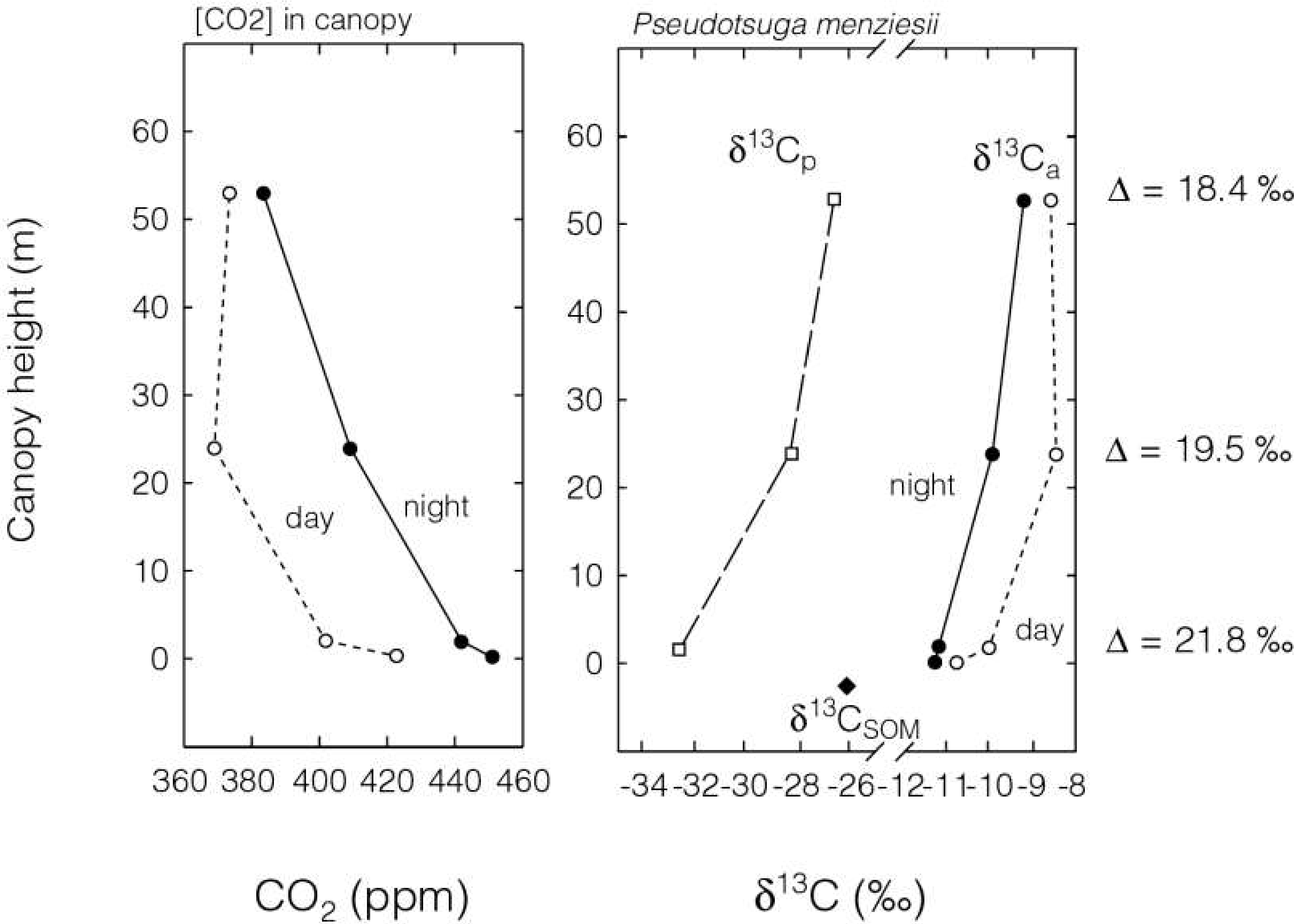


C_3 carbon isotope discrimination decreases with increased sunlight (PFD)



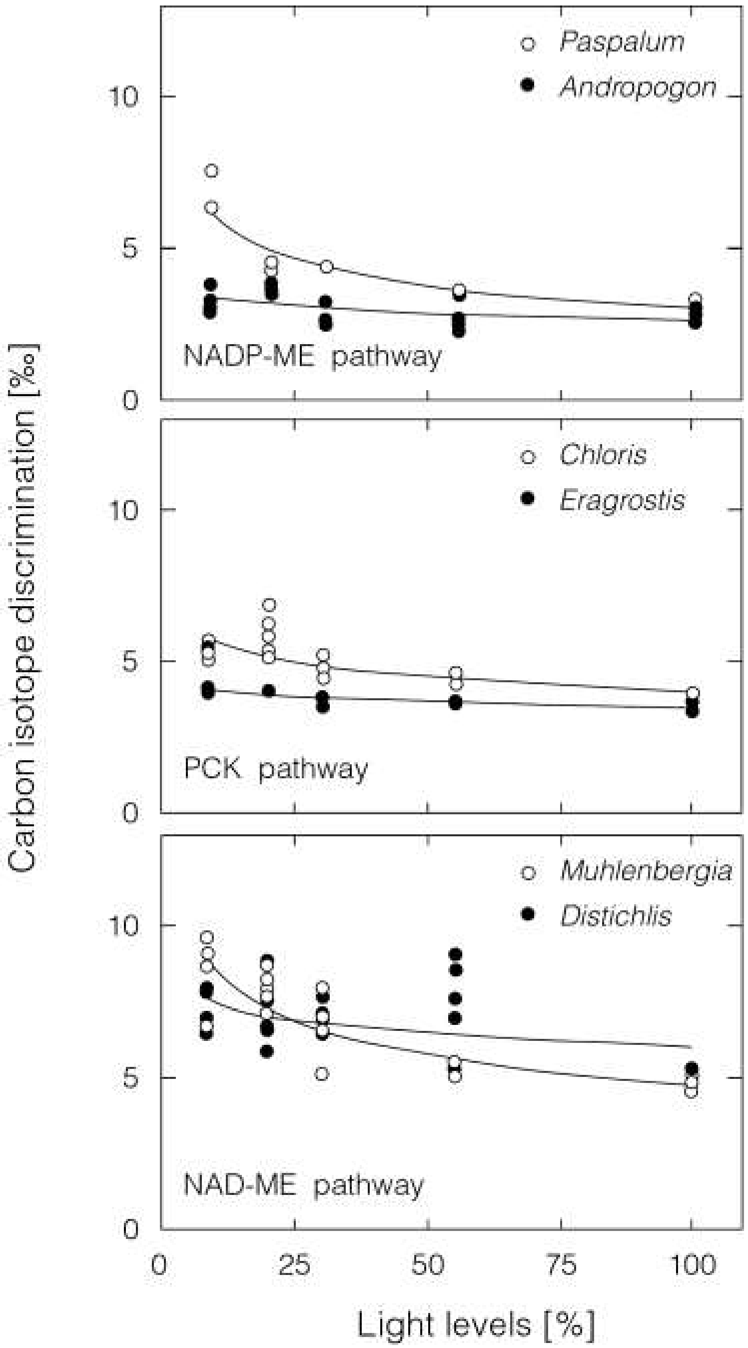
Ehleringer et al. (1986)

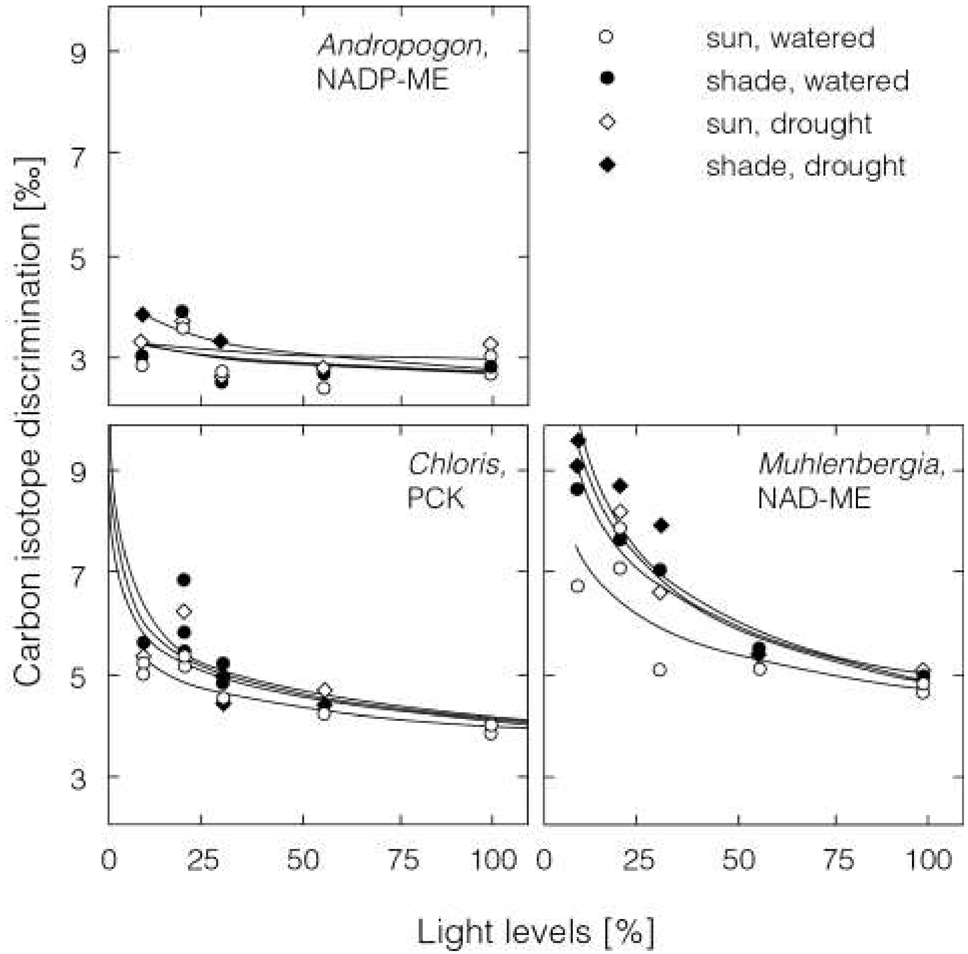
C_3 carbon isotope discrimination decreases with increased sunlight (PFD)



Fessenden and Ehleringer (2002)

C_4 carbon isotope discrimination decreases with increased sunlight (PFD)

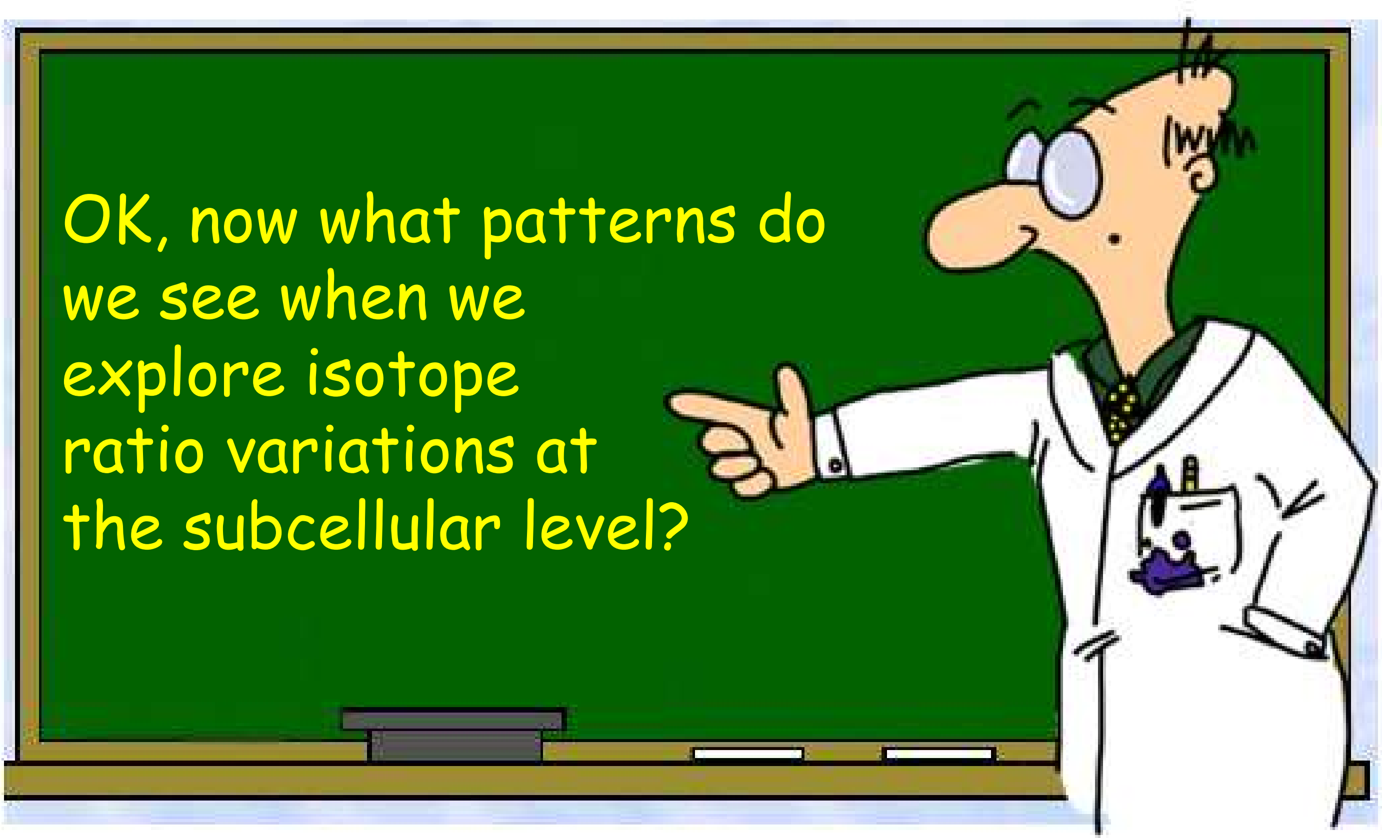




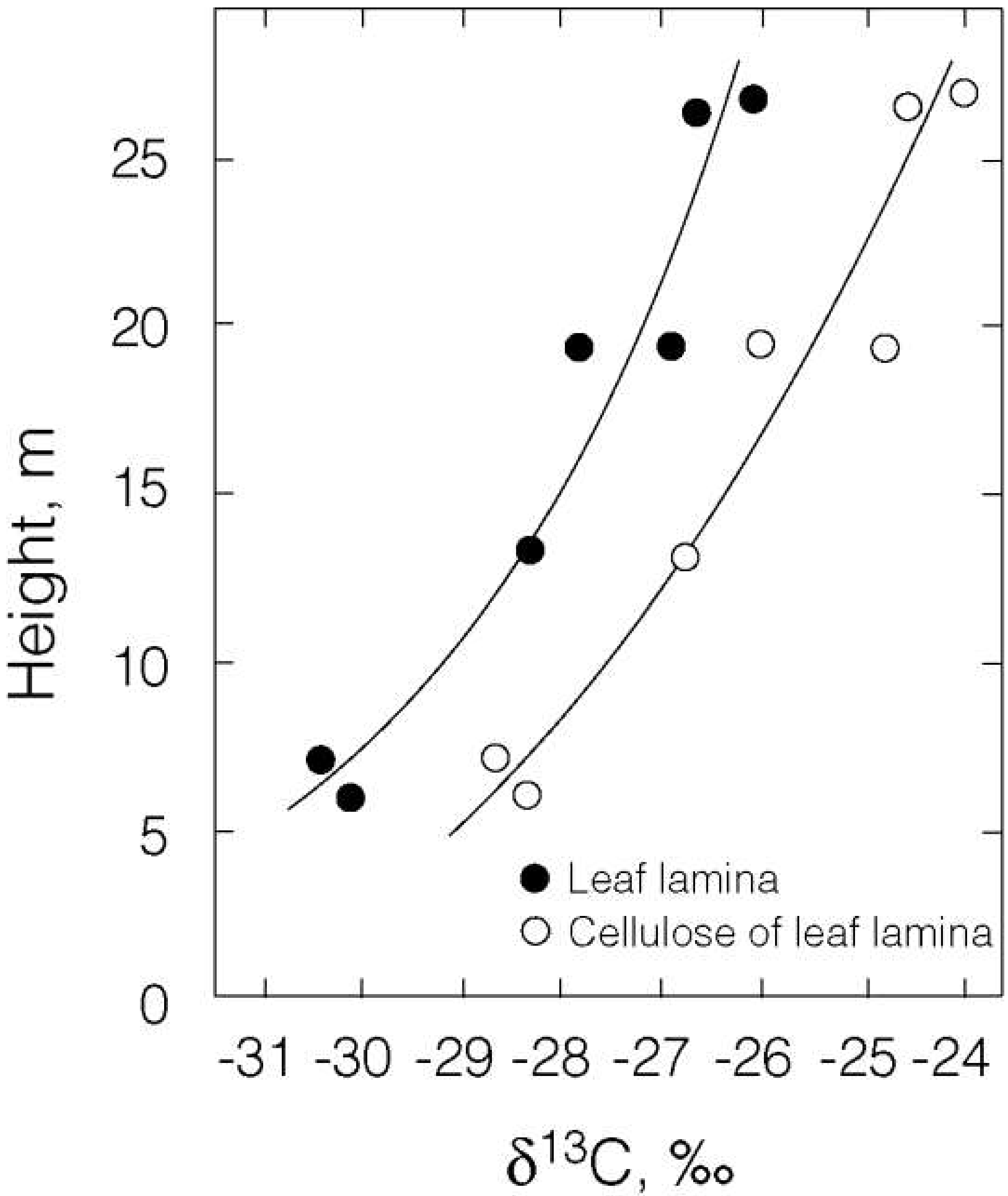
Buchmann et al. (1996)

Praktikum SS22
Biogeowissenschaften und Geographie
Im Zeitraum 14.3. - 18.4.

4.4.22 - 8.4.22
Abgabe Bericht 4 Wochen später


OK, now what patterns do we see when we explore isotope ratio variations at the subcellular level?

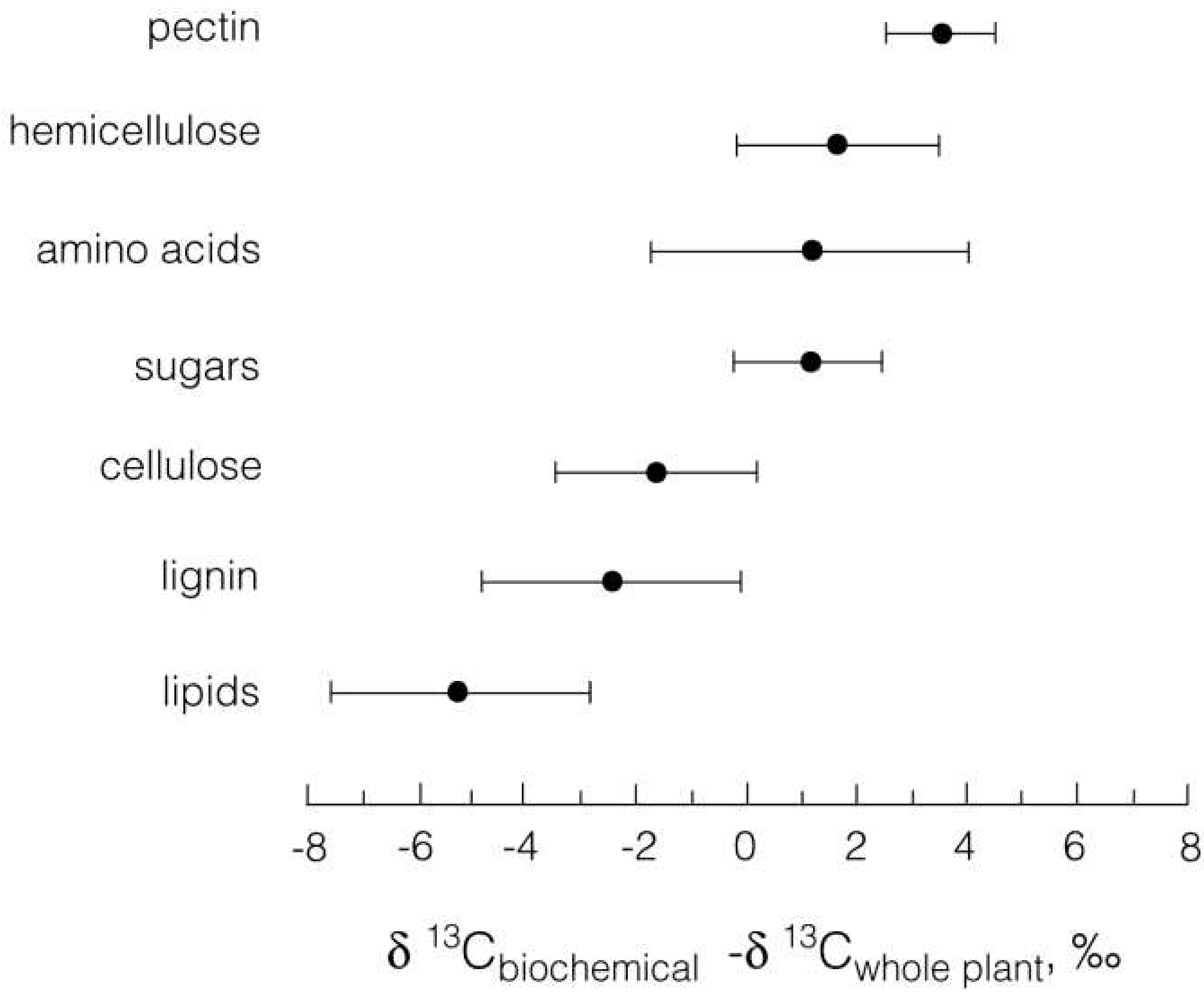
The are predictable intra-plant variations in ^{13}C



beech tree

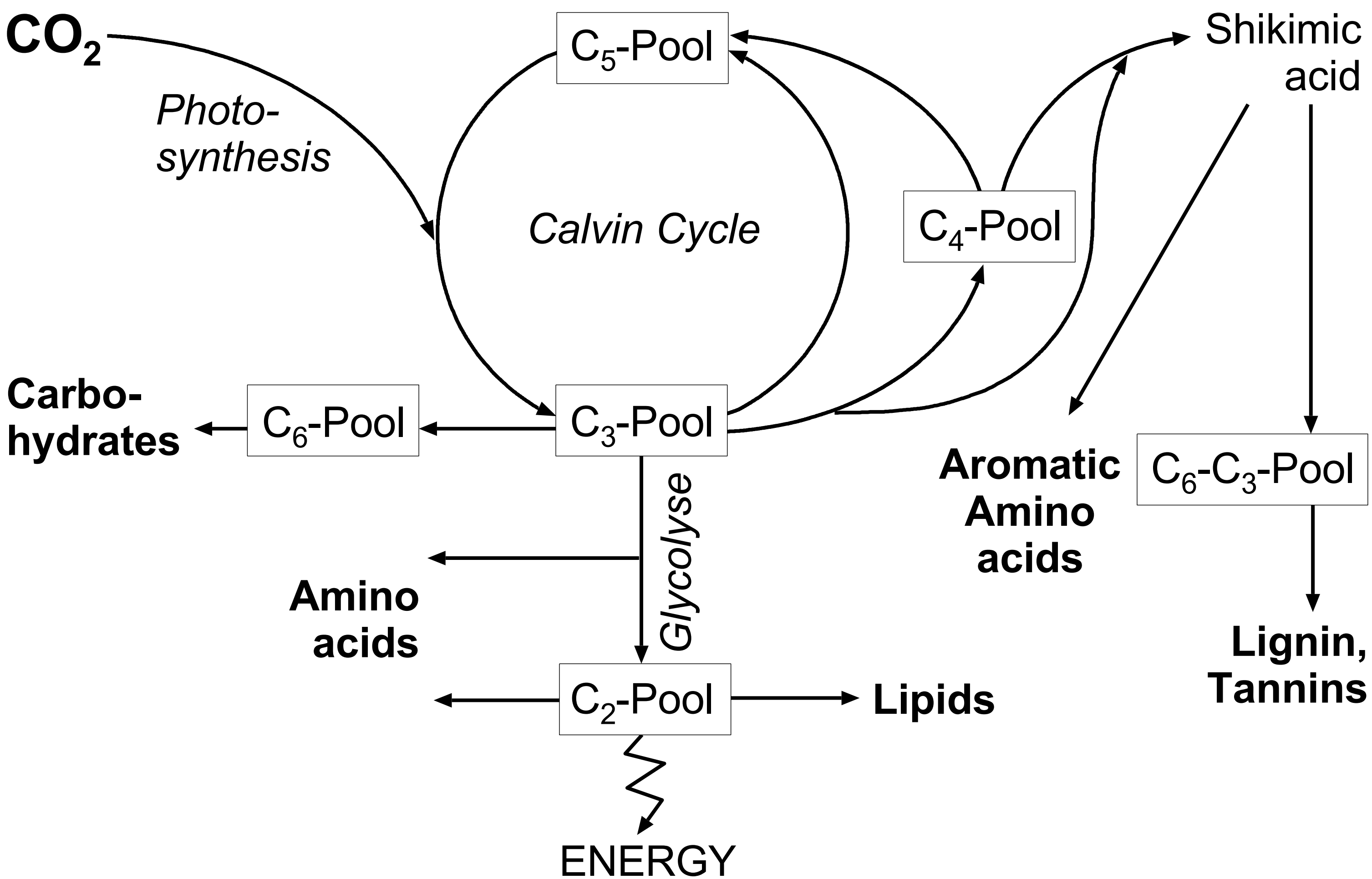
Leavitt and Long (1982)

Intermolecular variations in ^{13}C composition

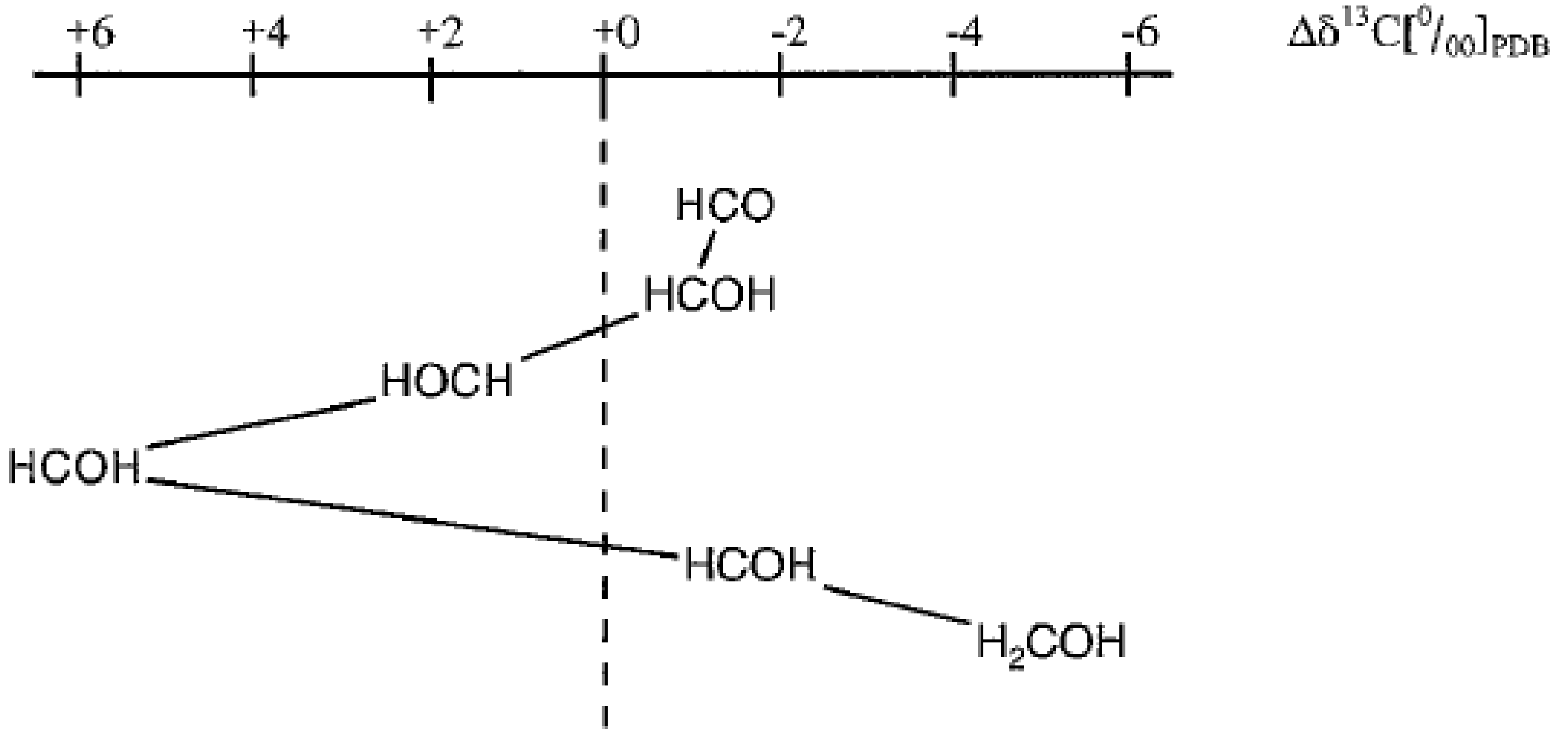


Boutton (1996)

Formation of Biomass



Intramolecular isotope variation



Gleixner and Schmidt (1997)

How can respired CO_2 be ^{13}C-enriched with respect to substrate δ^{13}C?

glucose: **C-C-C-C-C-C** = -25 ‰

^{13}C-enriched

pyruvate **C-C-C**

PDH

CO_2

^{13}C-enriched =
-21‰ (C-3 and C-4 positions)

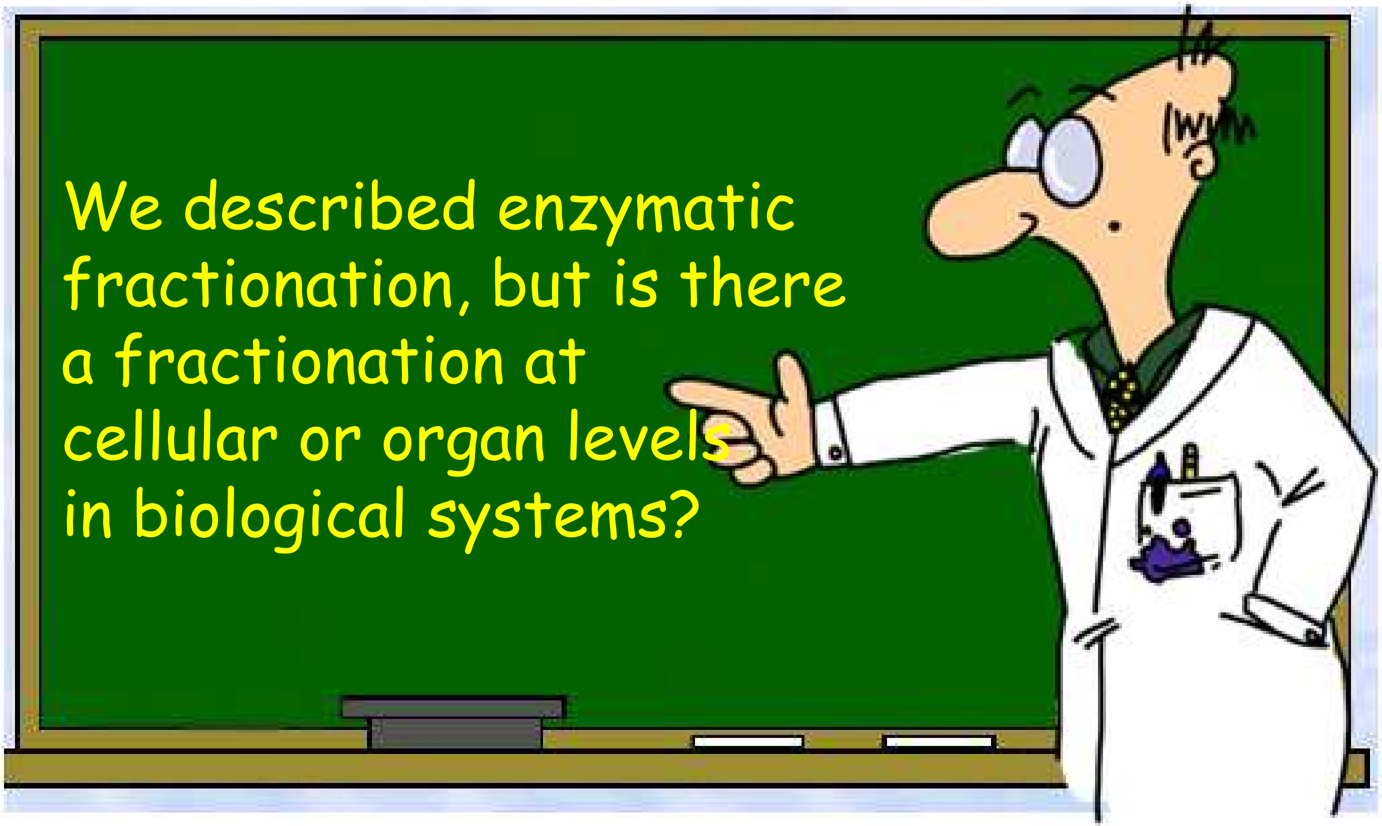
acetyl-CoA ⇄ e.g. Lipids

= -33‰

Krebs Cycle

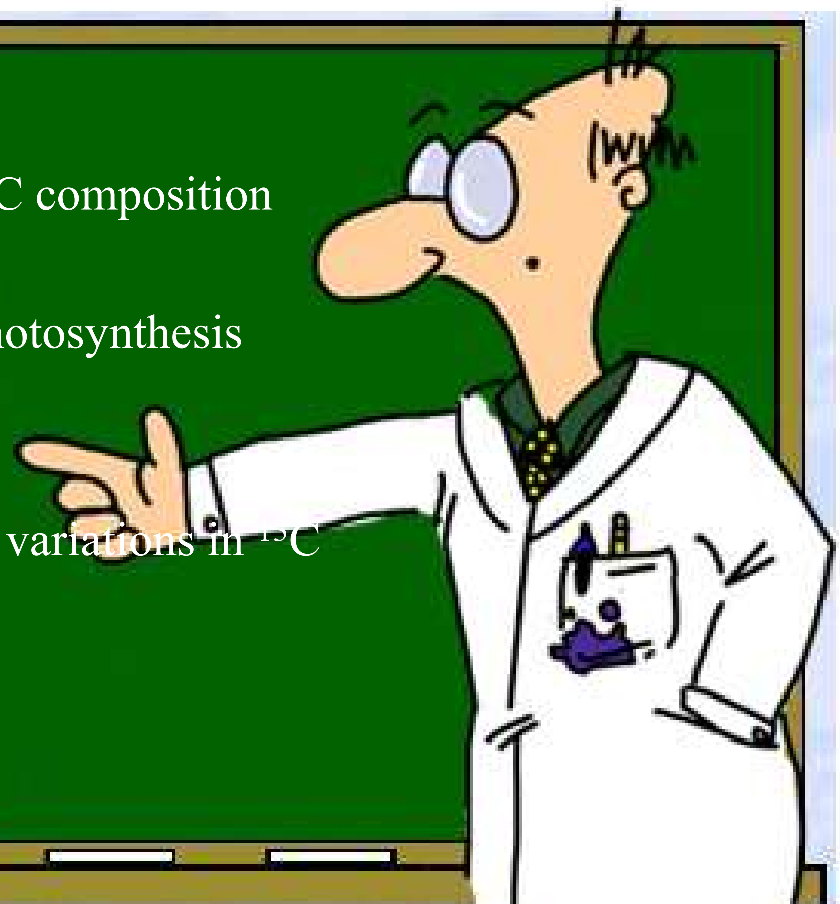
2 **CO_2** (-26‰) (C-2 and C-5)
(-28.5‰) (C-1 and C-6)

Short-term variation
in metabolic fluxes
may induce variability of
isotope ratio of
dark respired CO_2


We described enzymatic fractionation, but is there a fractionation at cellular or organ levels in biological systems?

Carbon isotope ratios in plants

Jim Ehleringer, University of Utah
Tel. 801-581-7623
E-mail: ehleringer@biology.utah.edu



Topics:

Molecular and tissue variations in ^{13}C composition

Phylogeny and ^{13}C

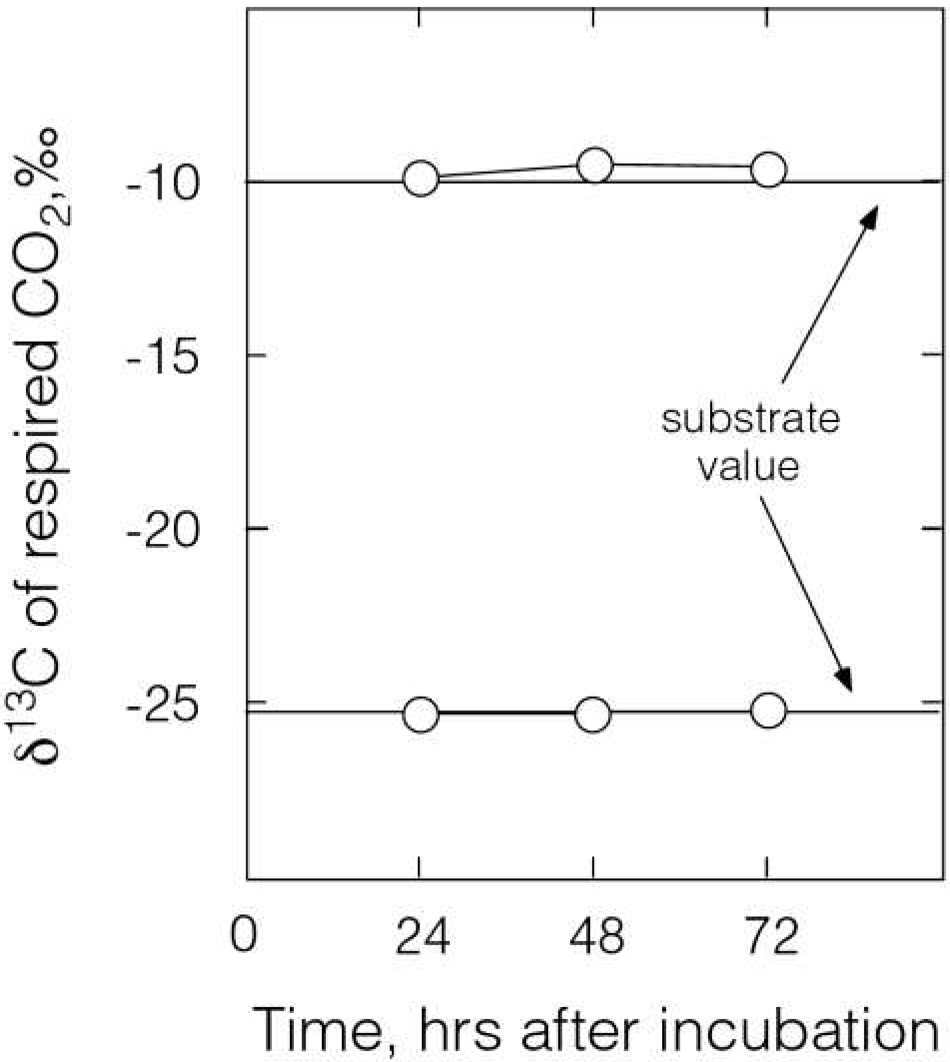
Rules for ^{13}C fractionation during photosynthesis

Ecological variations in ^{13}C

Respiration and decomposition

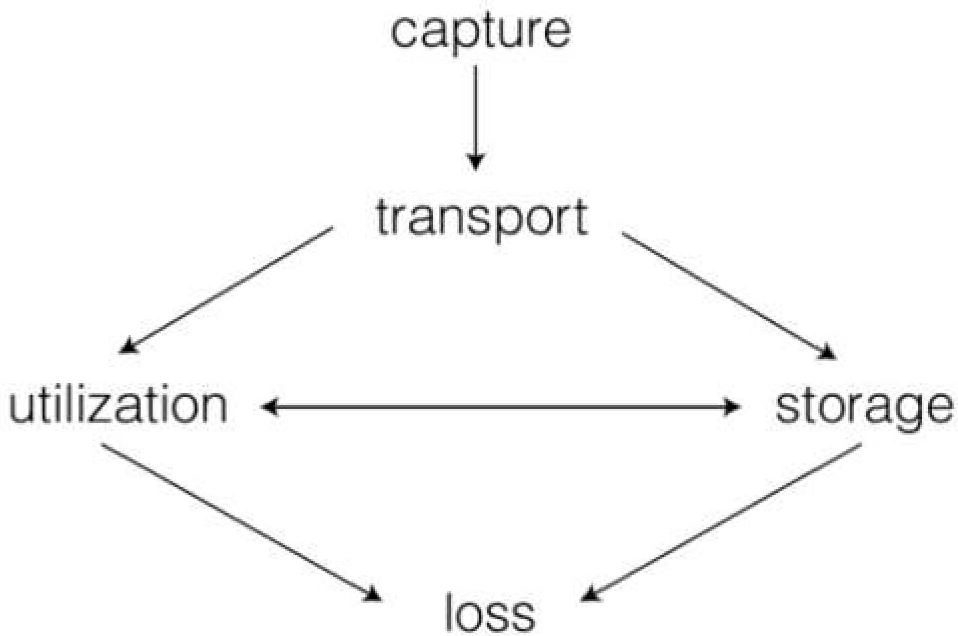
Population, genetic, and agricultural variations in ^{13}C

During mitochondrial respiration, there appears to be no fractionation



Lin and Ehleringer (1997)

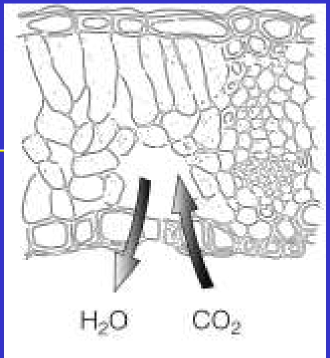
There is no theory for processes at the organ- and/or whole-plant levels



Is transported carbon isotopically heavier than leaves?

Factors influencing isotopic content of ecosystem respiration

stomatal conductance



c_i/c_a

photosynthesis

$\delta^{13}C$ of fixed carbon

faster (days)

foliar respiration

shoot respiration

root/rhizosphere respiration

decomp of SOM

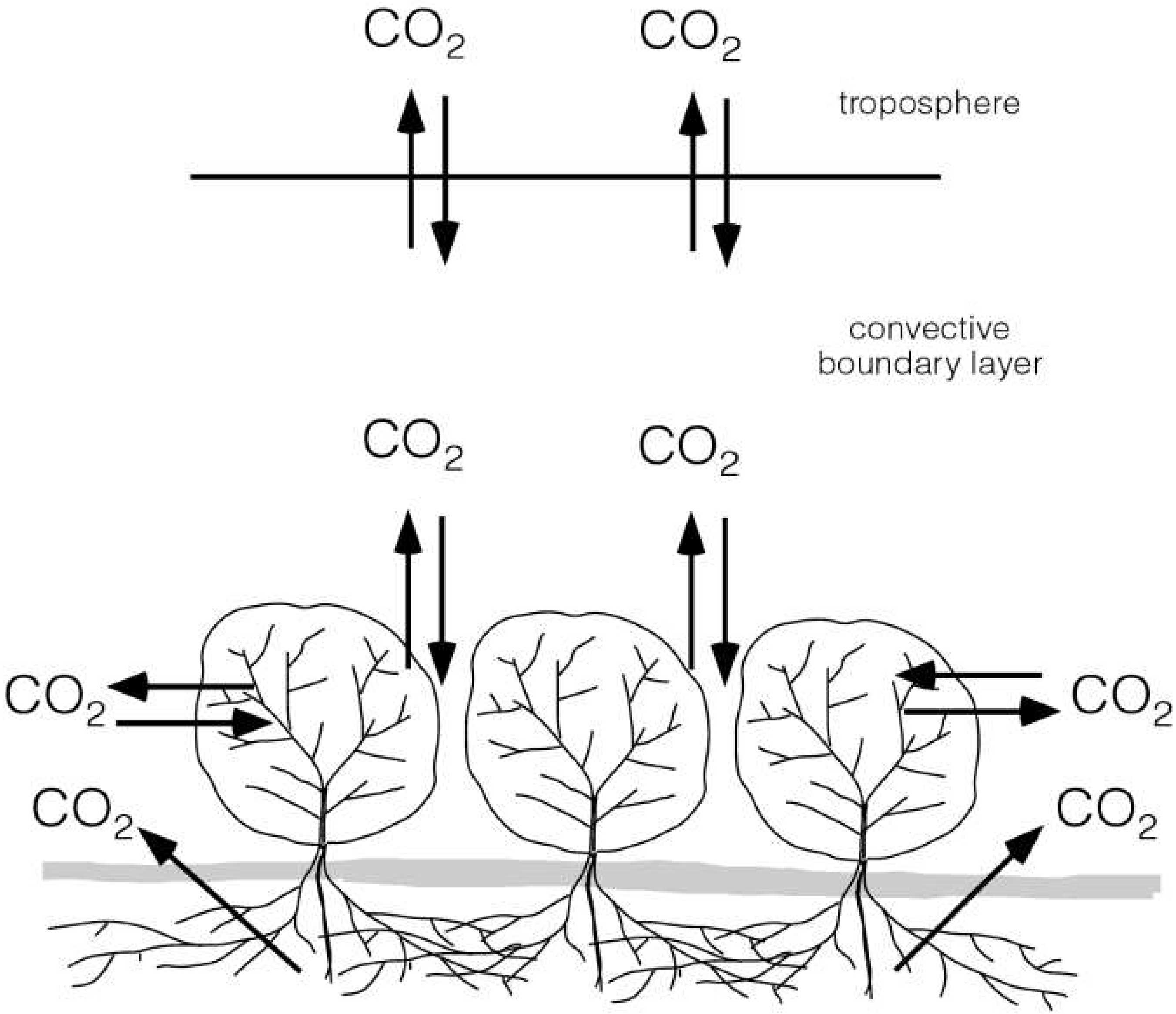
slower (years to decades)

$\delta^{13}C$ of respired CO_2

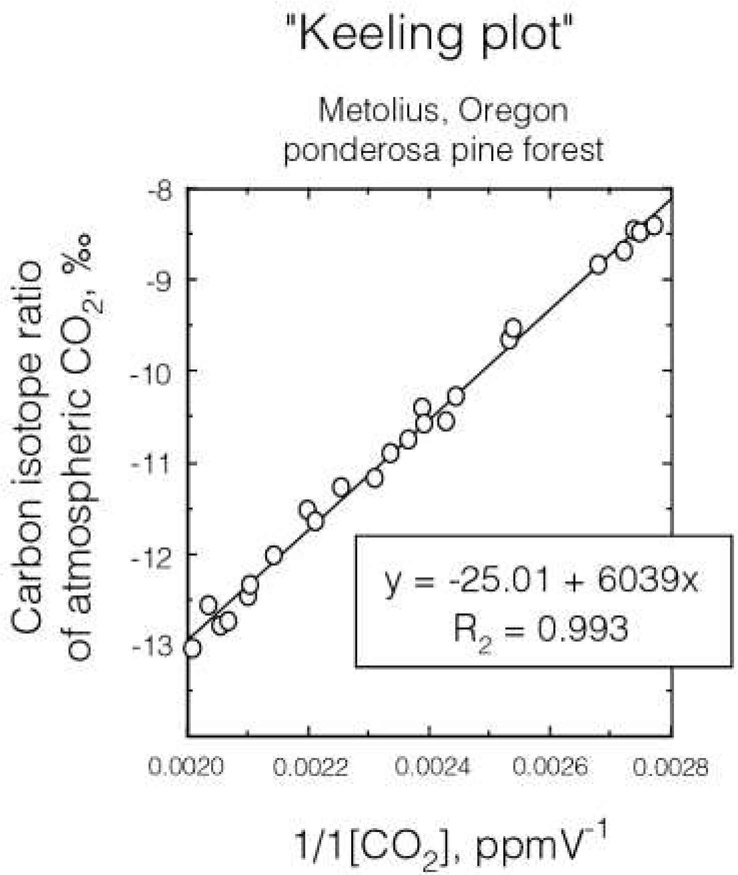
What is the difference between a time-lag versus a fractionation?

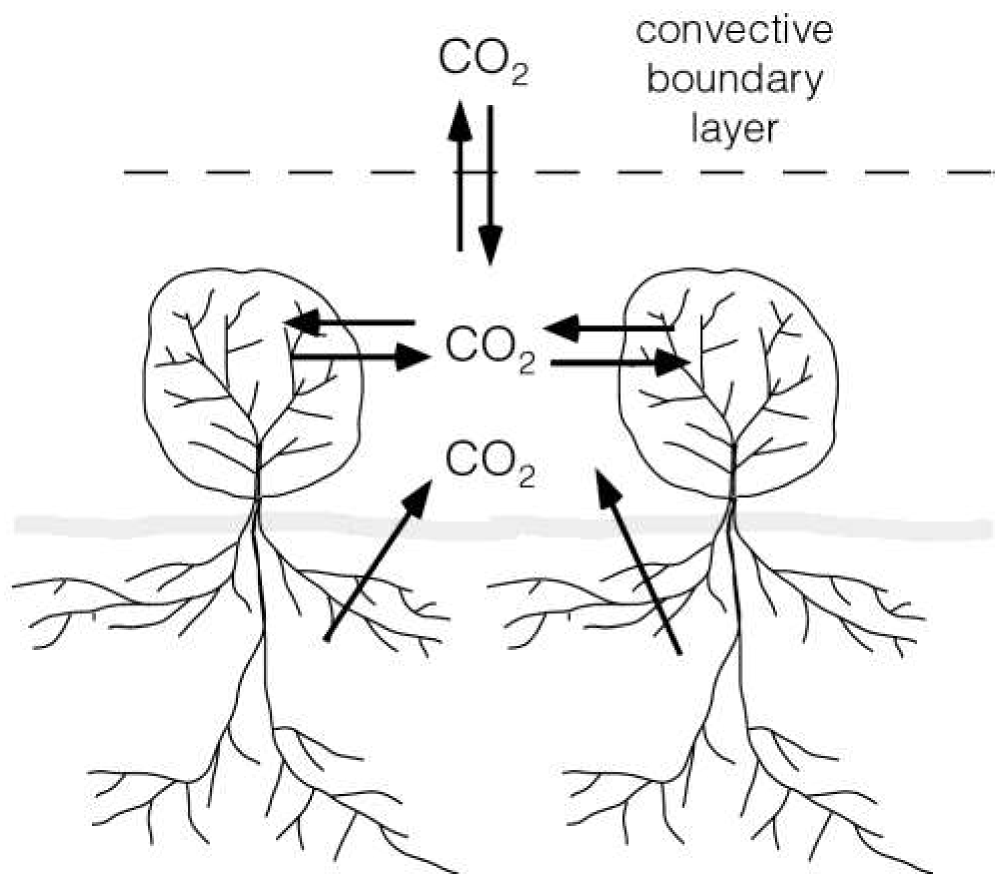
Are there isotopic differences that become irrelevant at the larger spatial scales?

We can scale respiratory ^{13}C processes from leaf to ecosystem

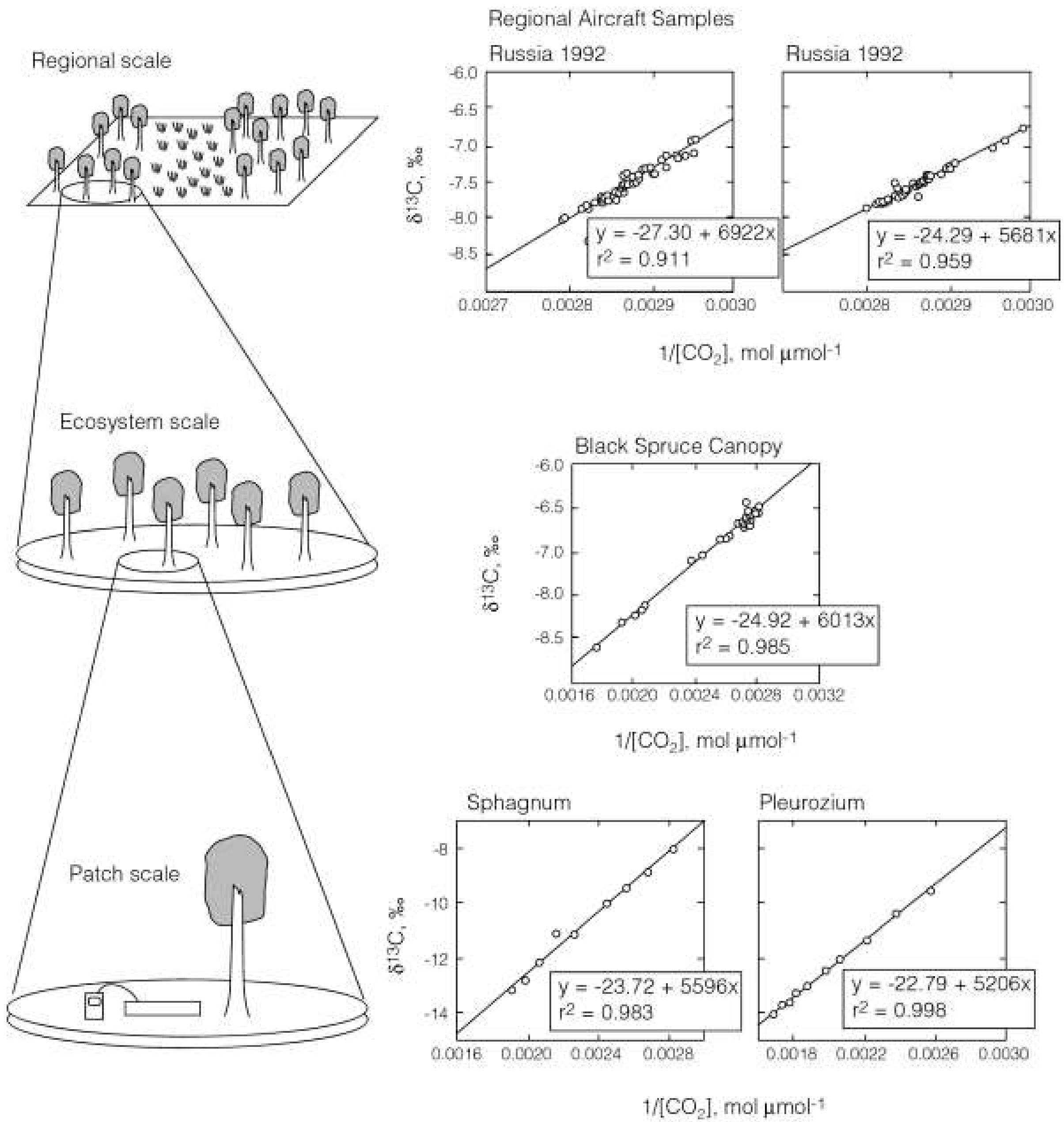


The "Keeling plot" allows us to get ecosystem ^{13}C respiration values

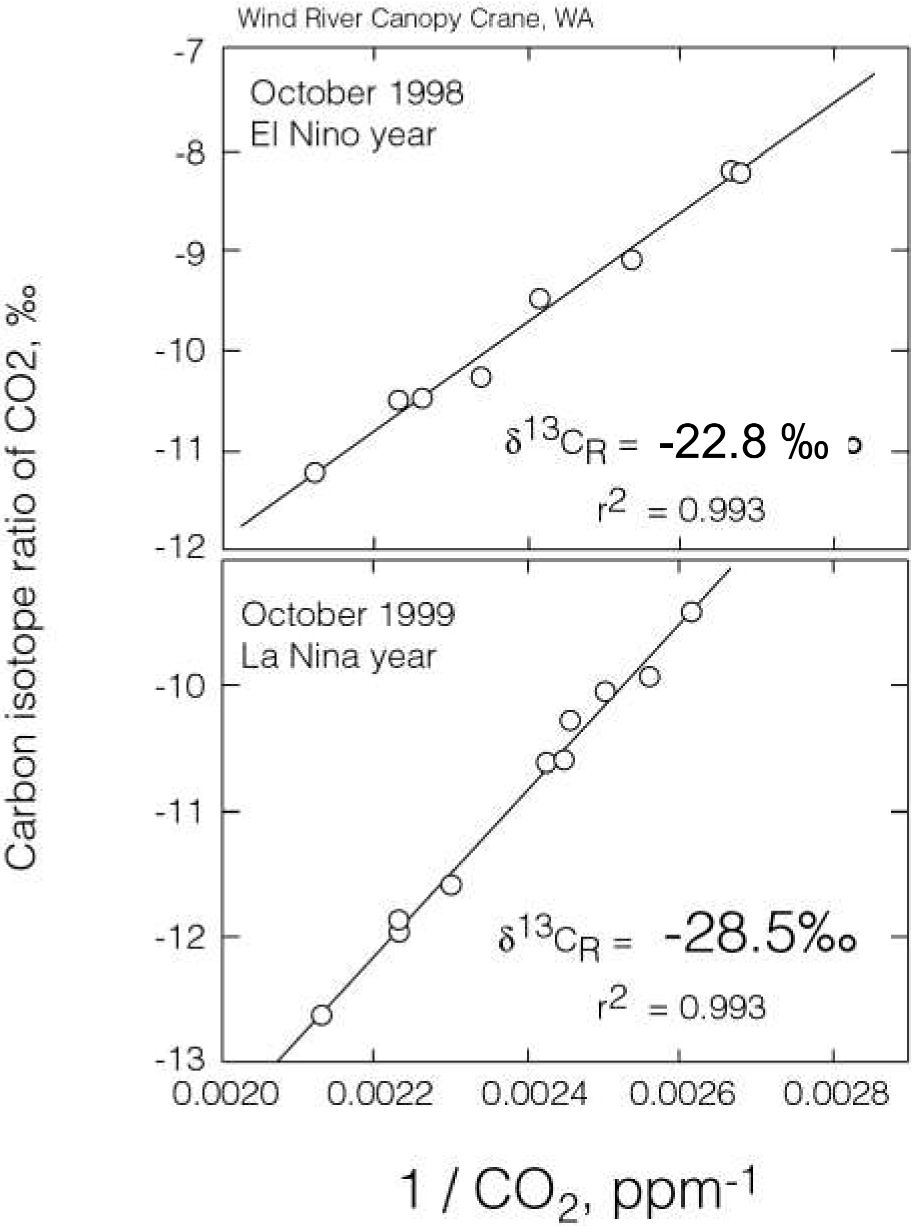


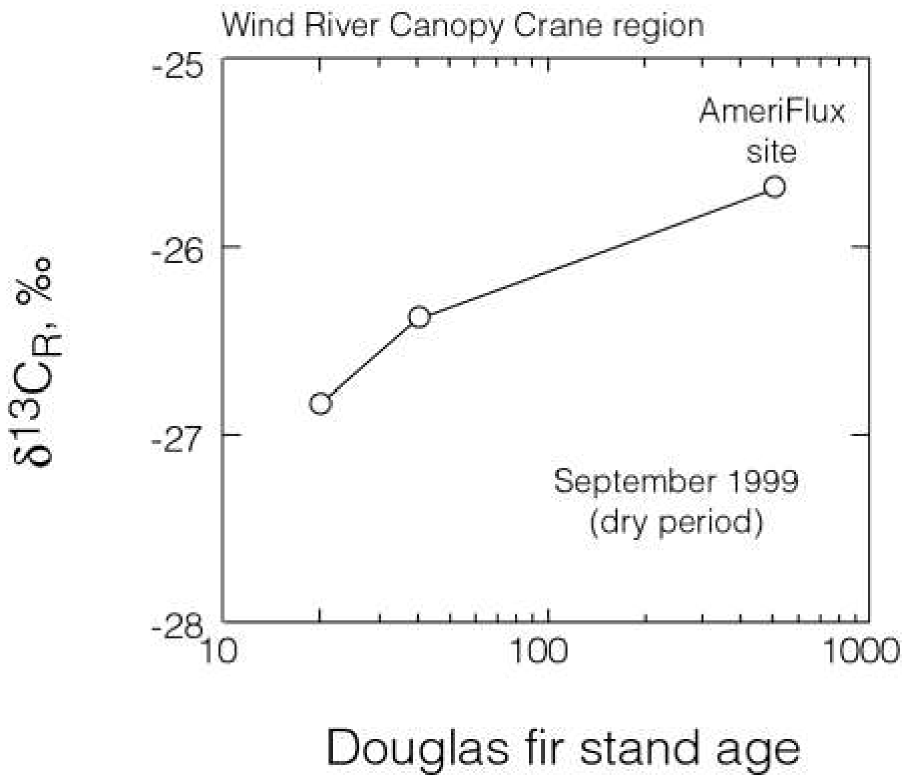


Boreal Forest Example



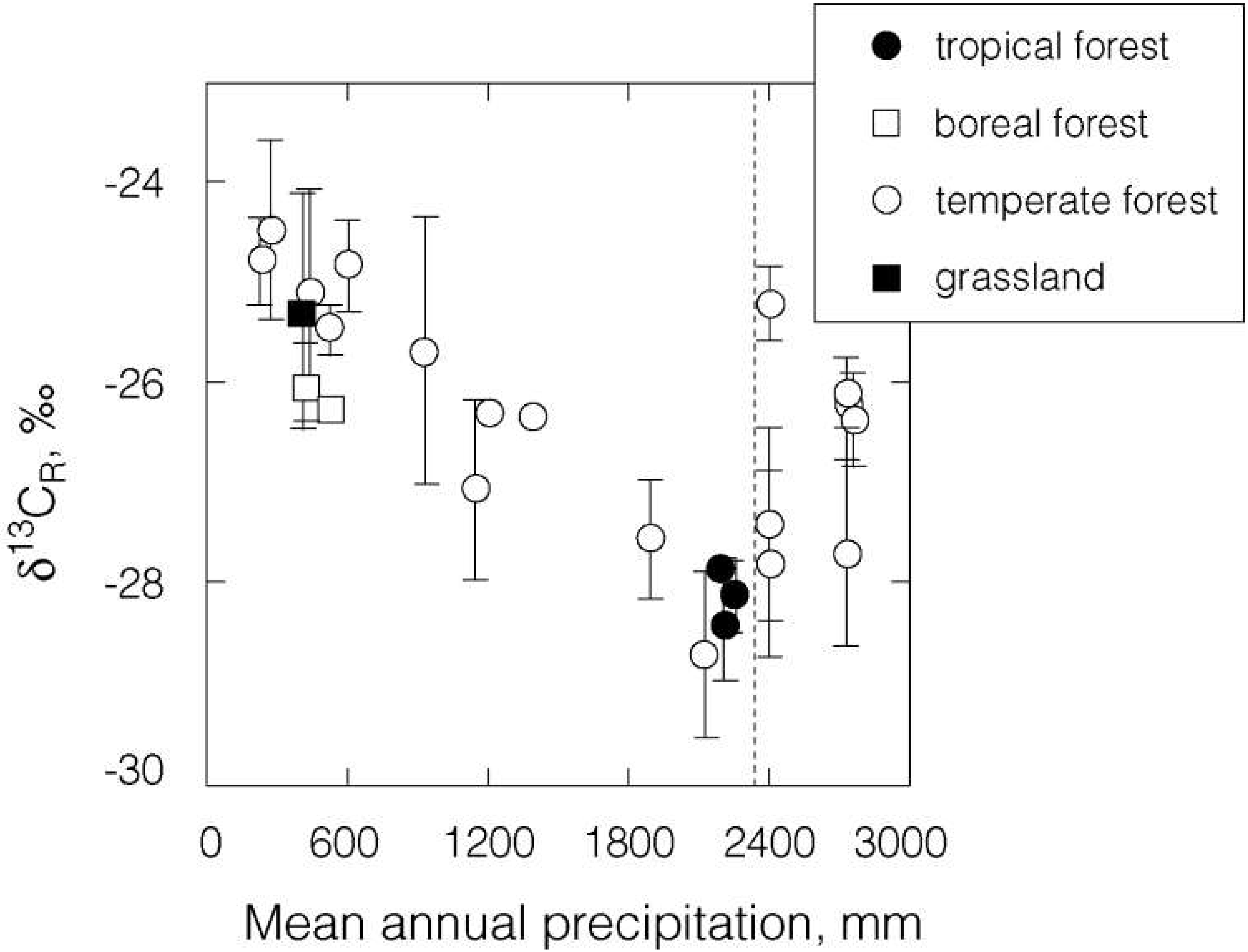
Ecosystem ^{13}C respiration values respond to drought (el nino) and stand ag





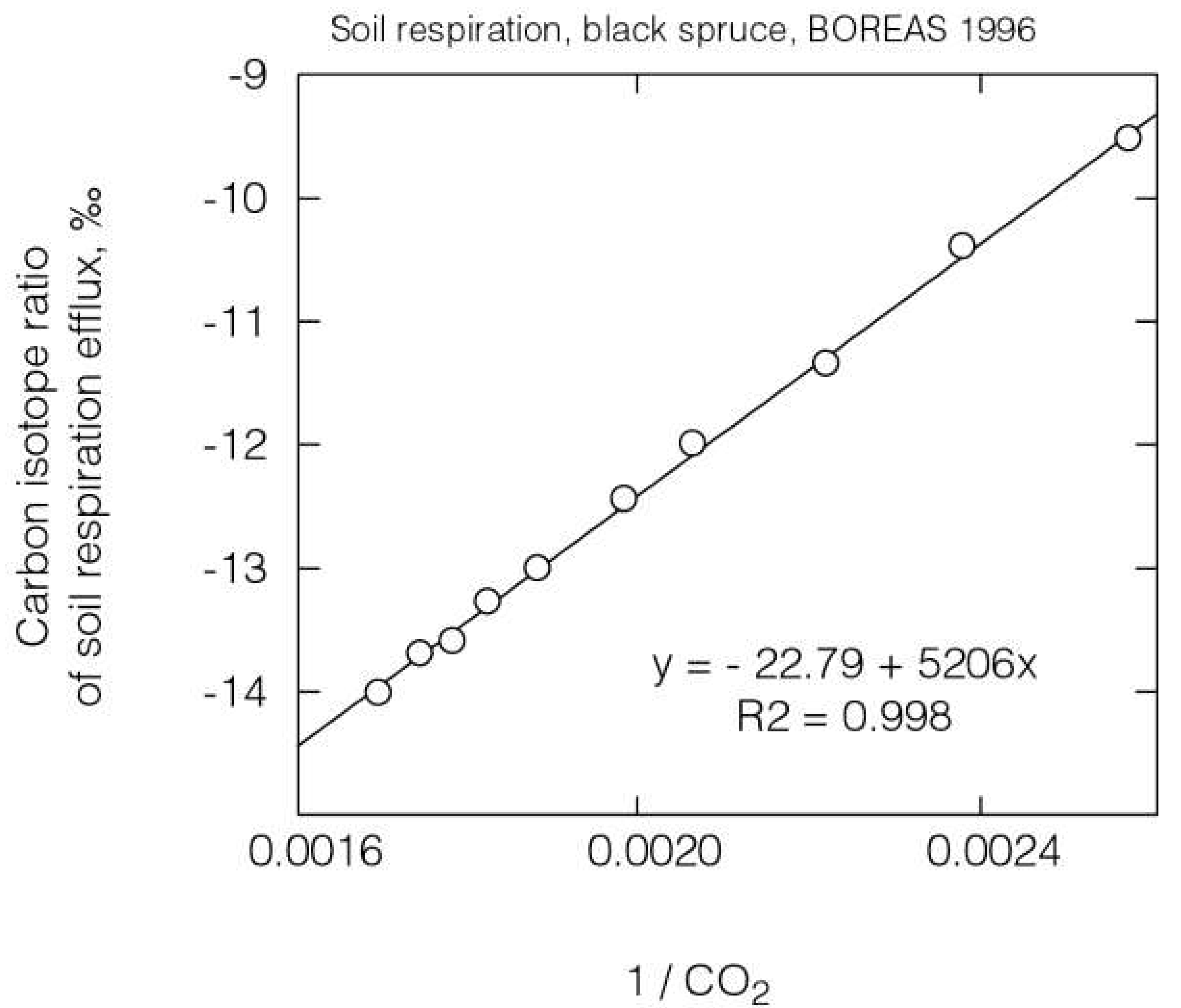
Fessenden and Ehleringer (2002)

^{13}C of ecosystem respiration responds to drought across biomes



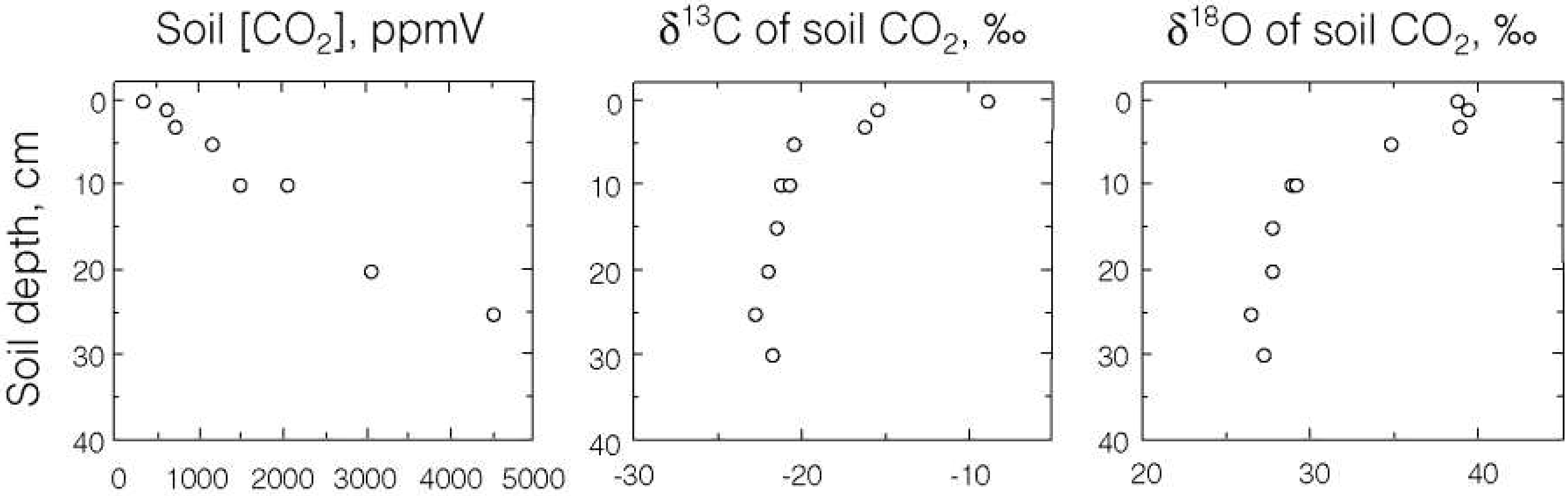
Pataki et al. (2003)

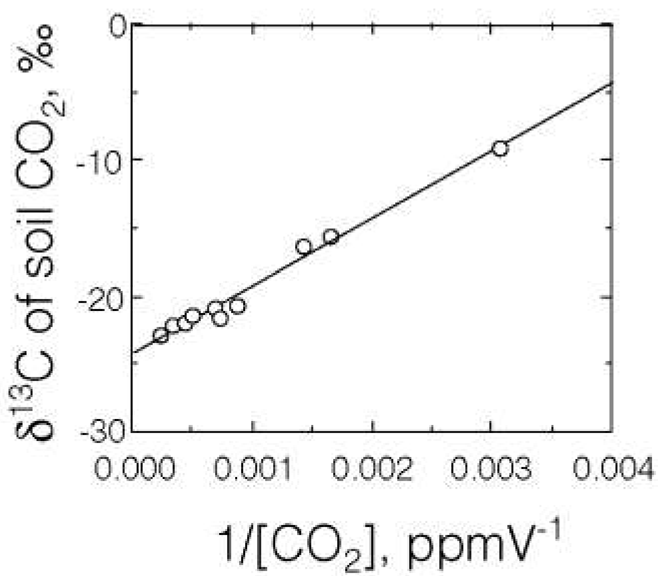
The Keeling plot approach can be used to estimate ^{13}C of soil efflux



Flanagan et al. (1998)

Soil $^{13}C^{18}O^{16}O$ profiles

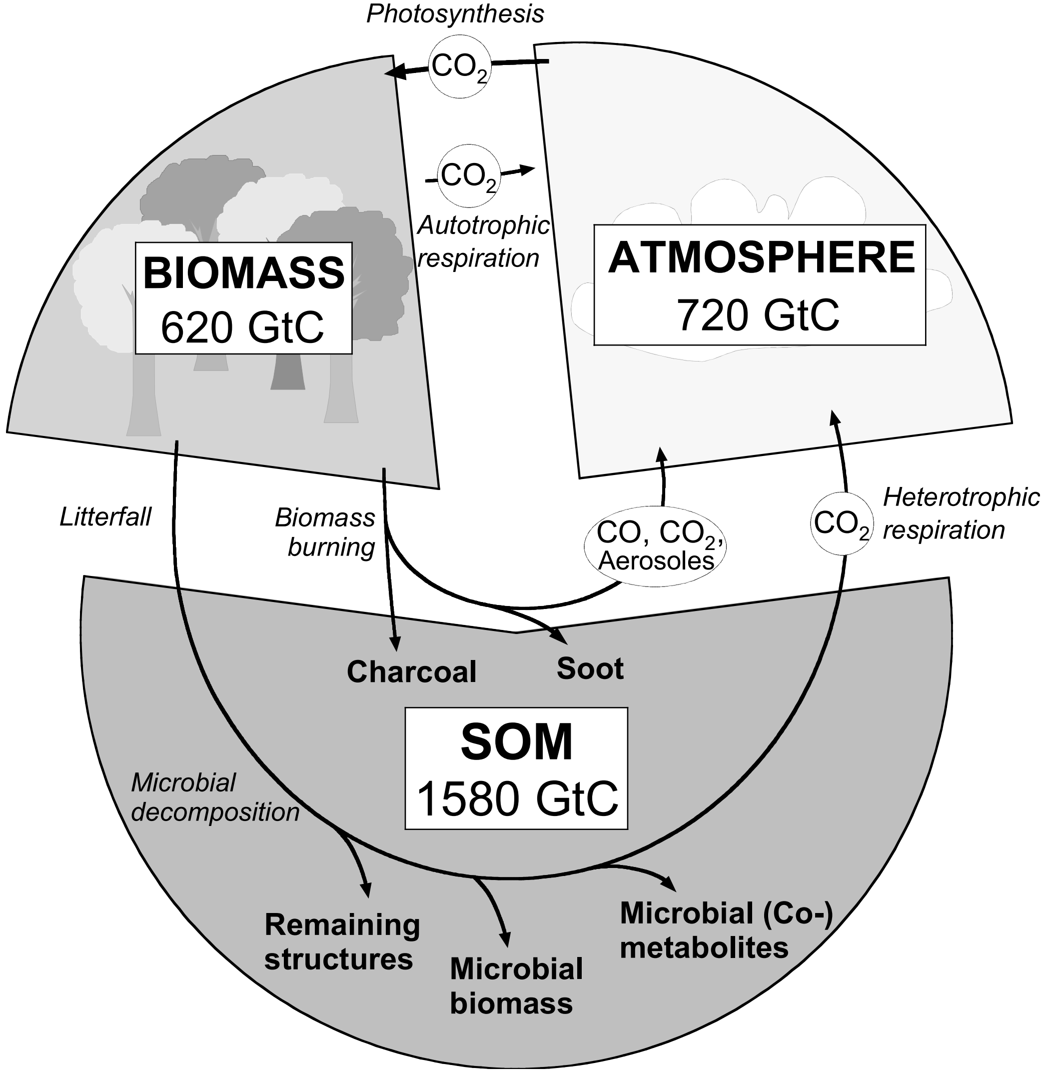




$y = -24.1 + 4981x$, $R^2 = 0.983$

Why SOM

Terrestrial Carbon Cycle

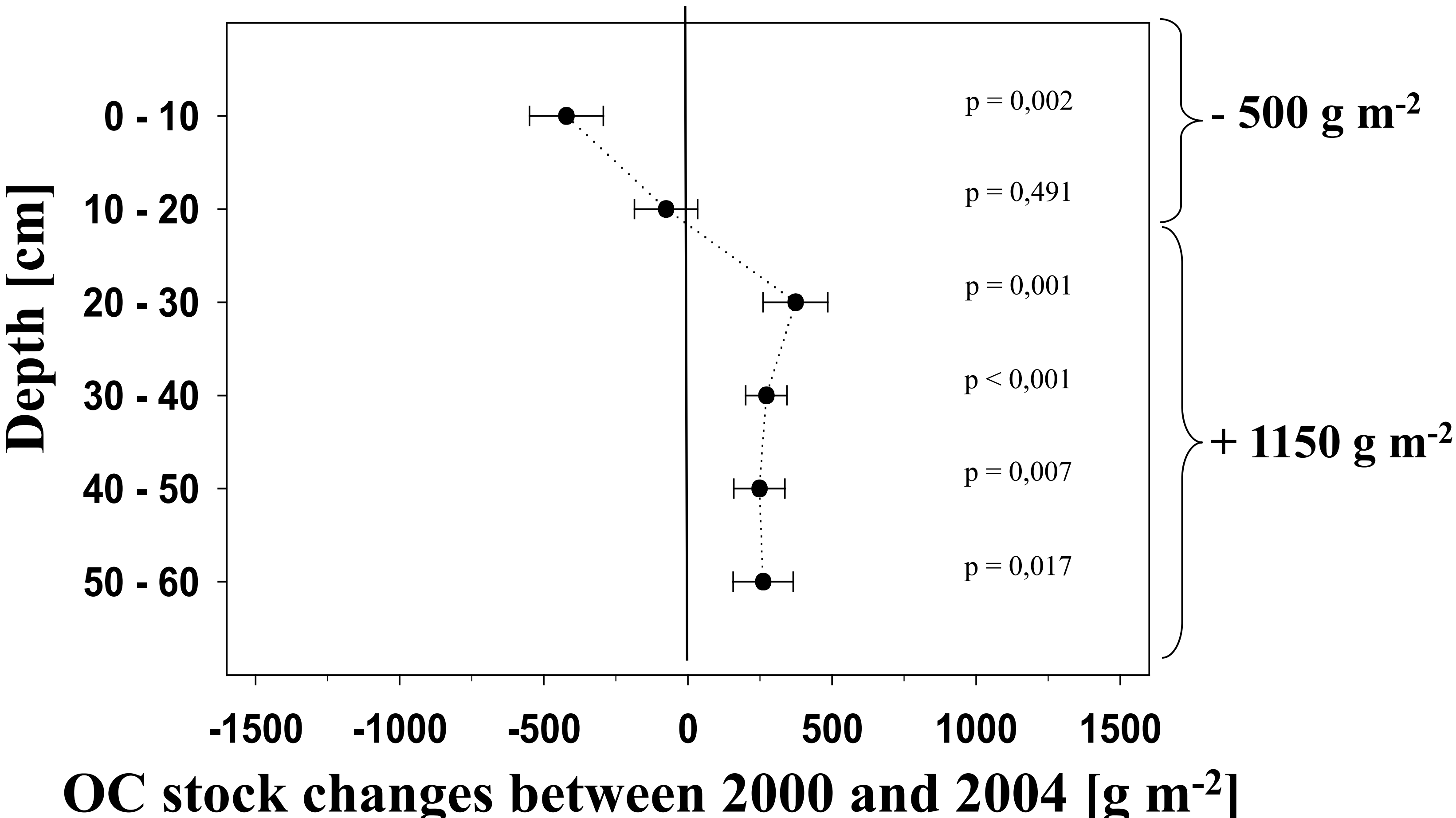


Gleixner et al., 2001

Old Growth Forest - National

Changes of soil organic carbon stocks in the Hainich – NP years 2000 and 2004, n = 80, paired sampling

Annual increase ≈ 160 g C/m²



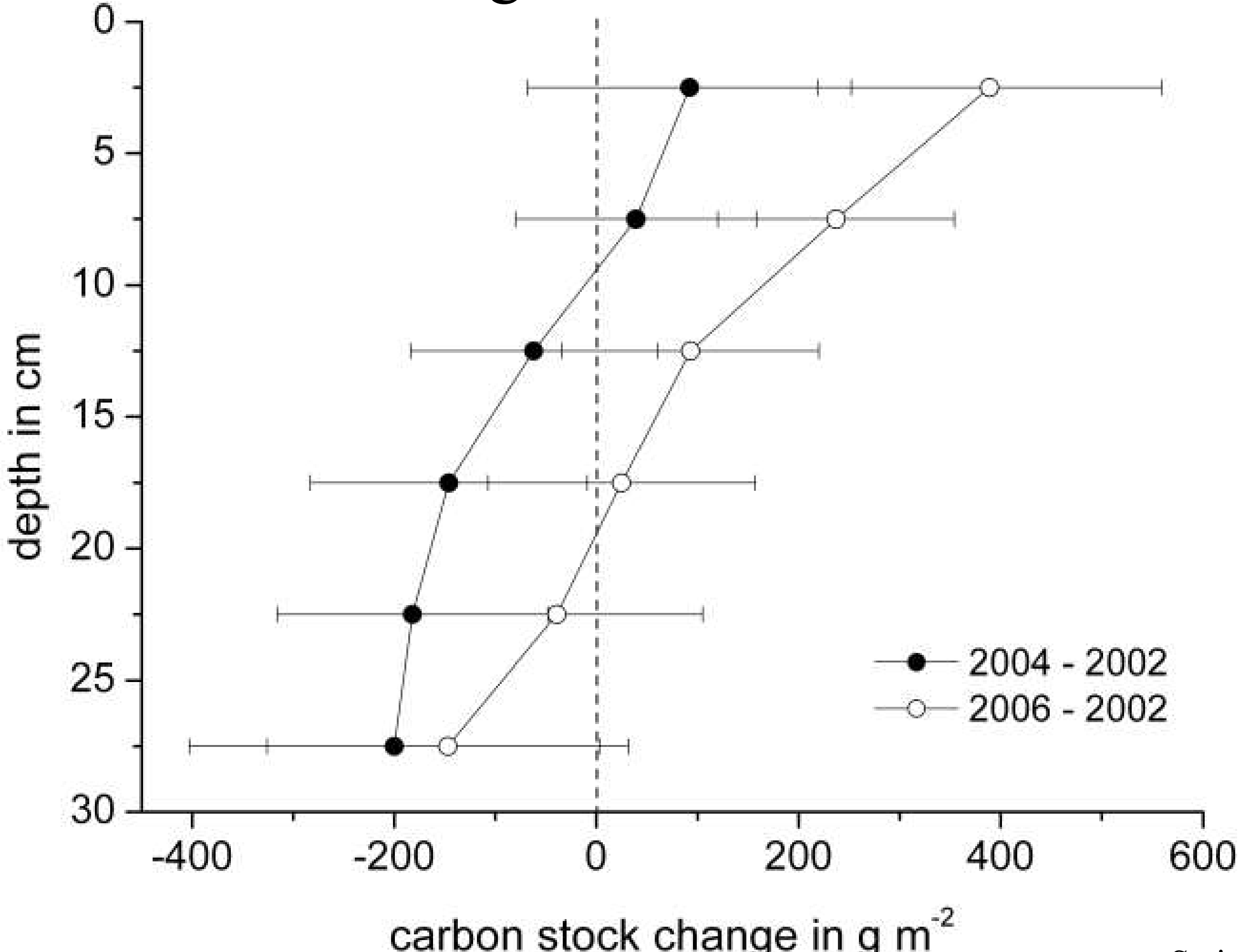
Gleixner et al., 2009

The Jena Experiment

Rate of C stock changes

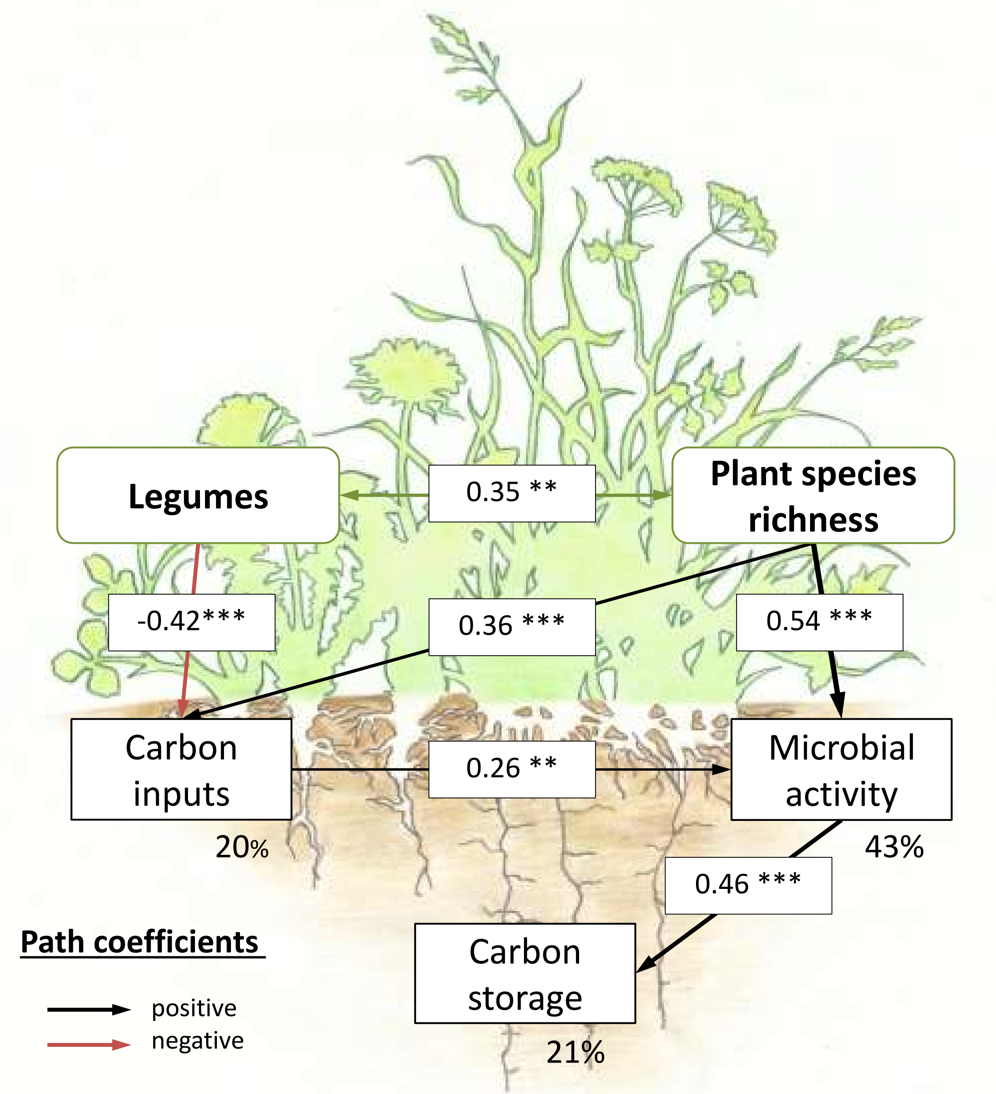
Annual increase of carbon stocks

50 – 190 g C/m^2



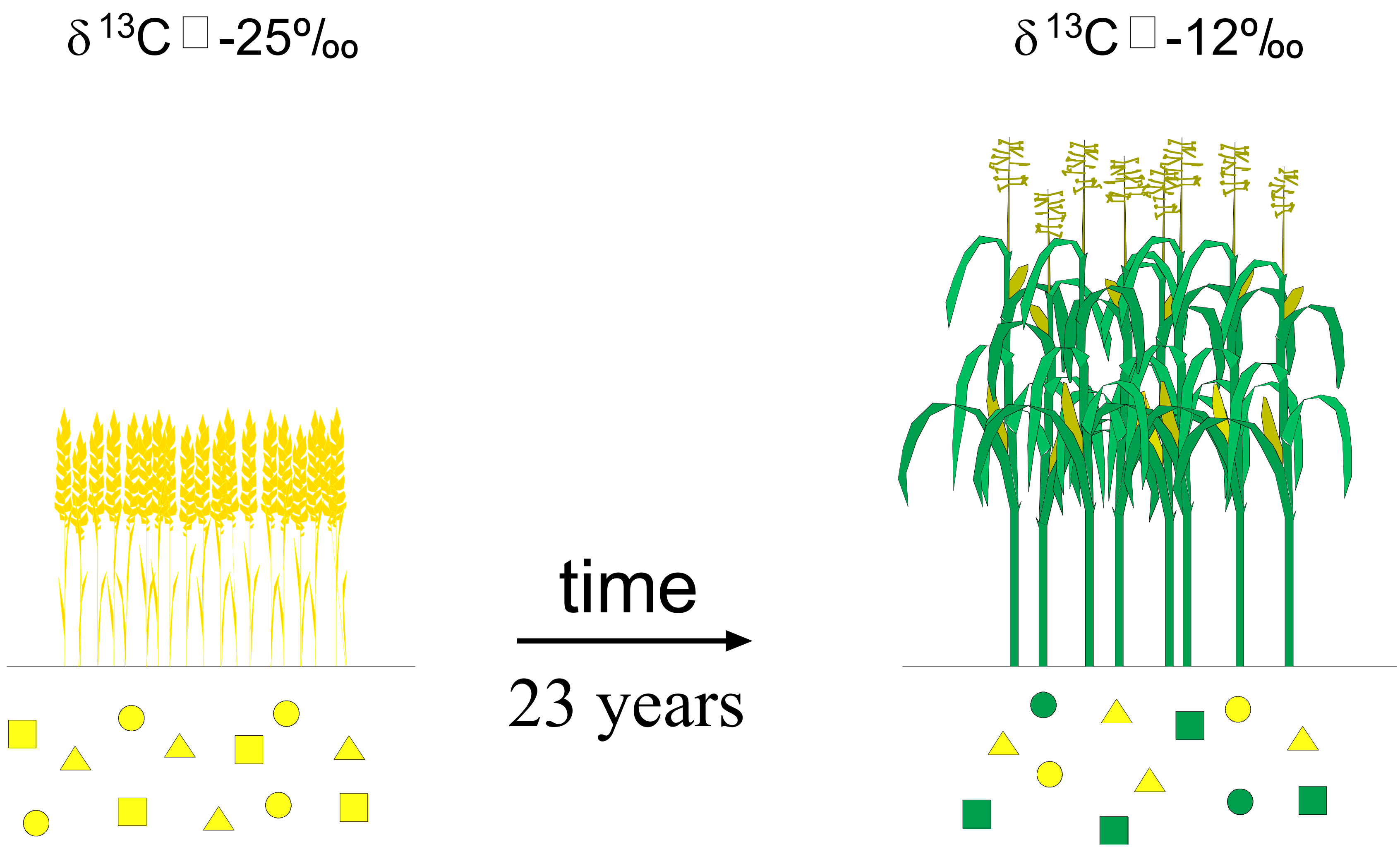
Steinbeiß et al., GCB 08

Microbial Carbon Storage

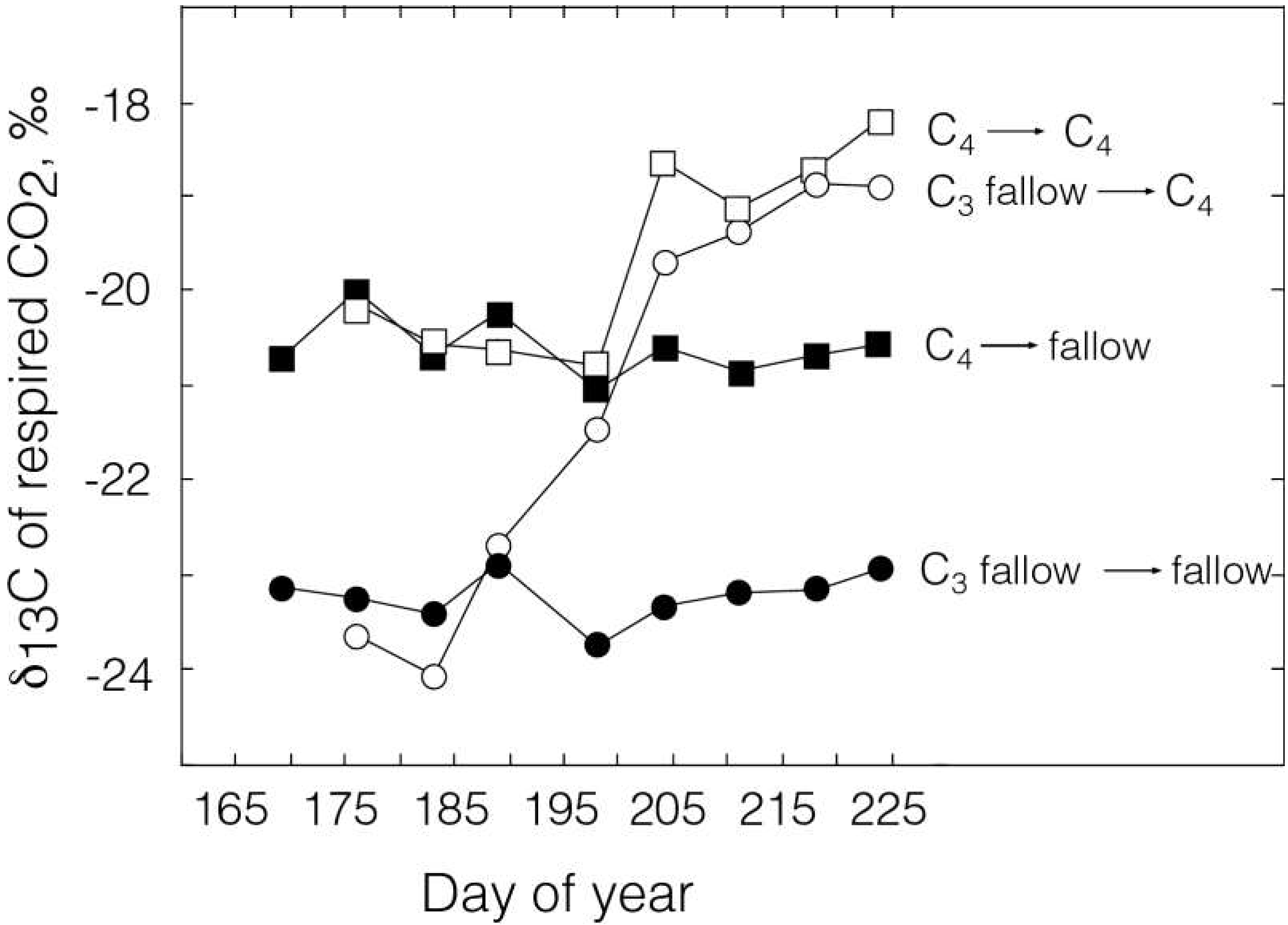


Lange et al., Nat.Com. 15

Natural Labeling Experiment

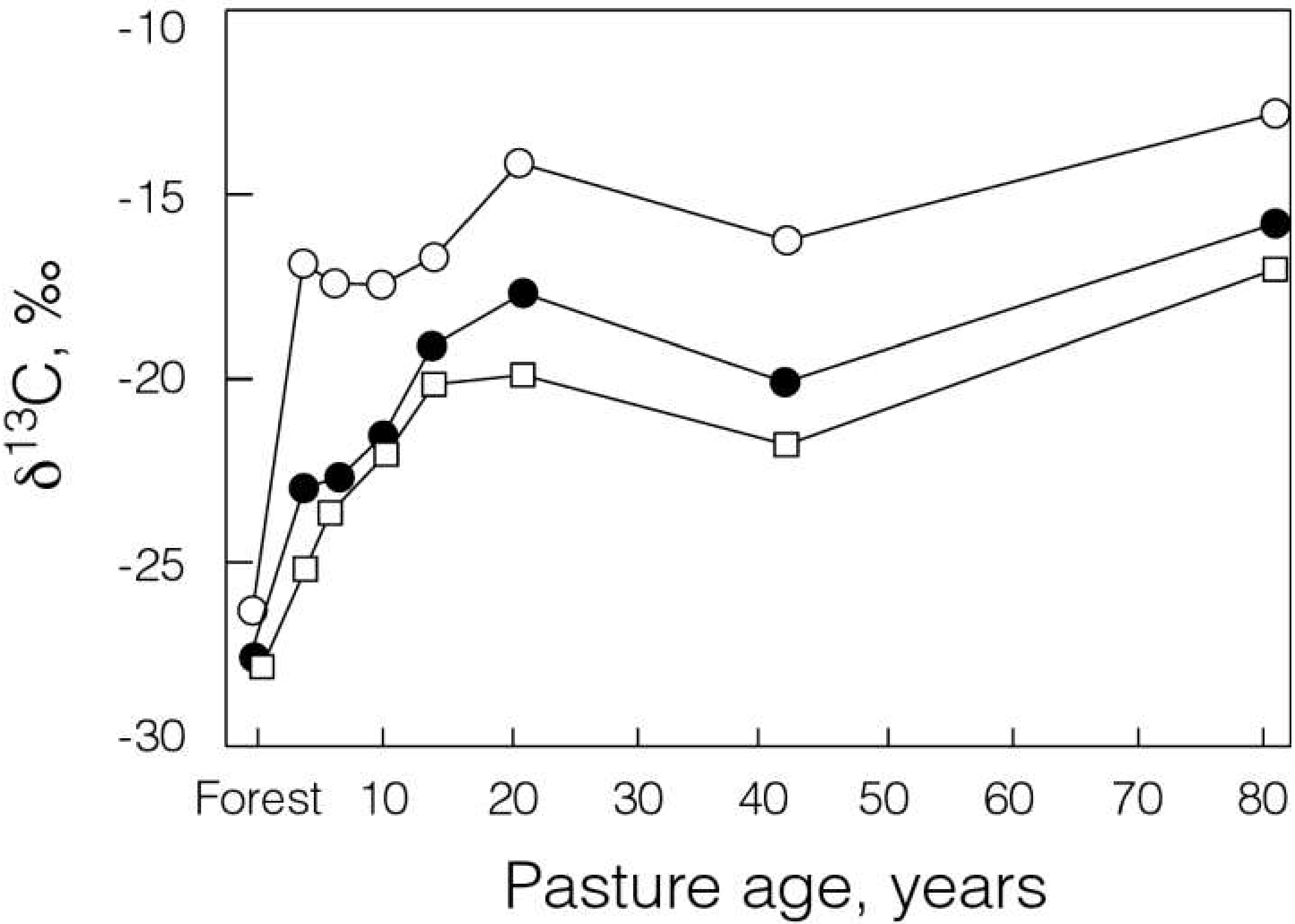


Soil $^{13}CO_2$ efflux measurements indicate a rapid cycling C component



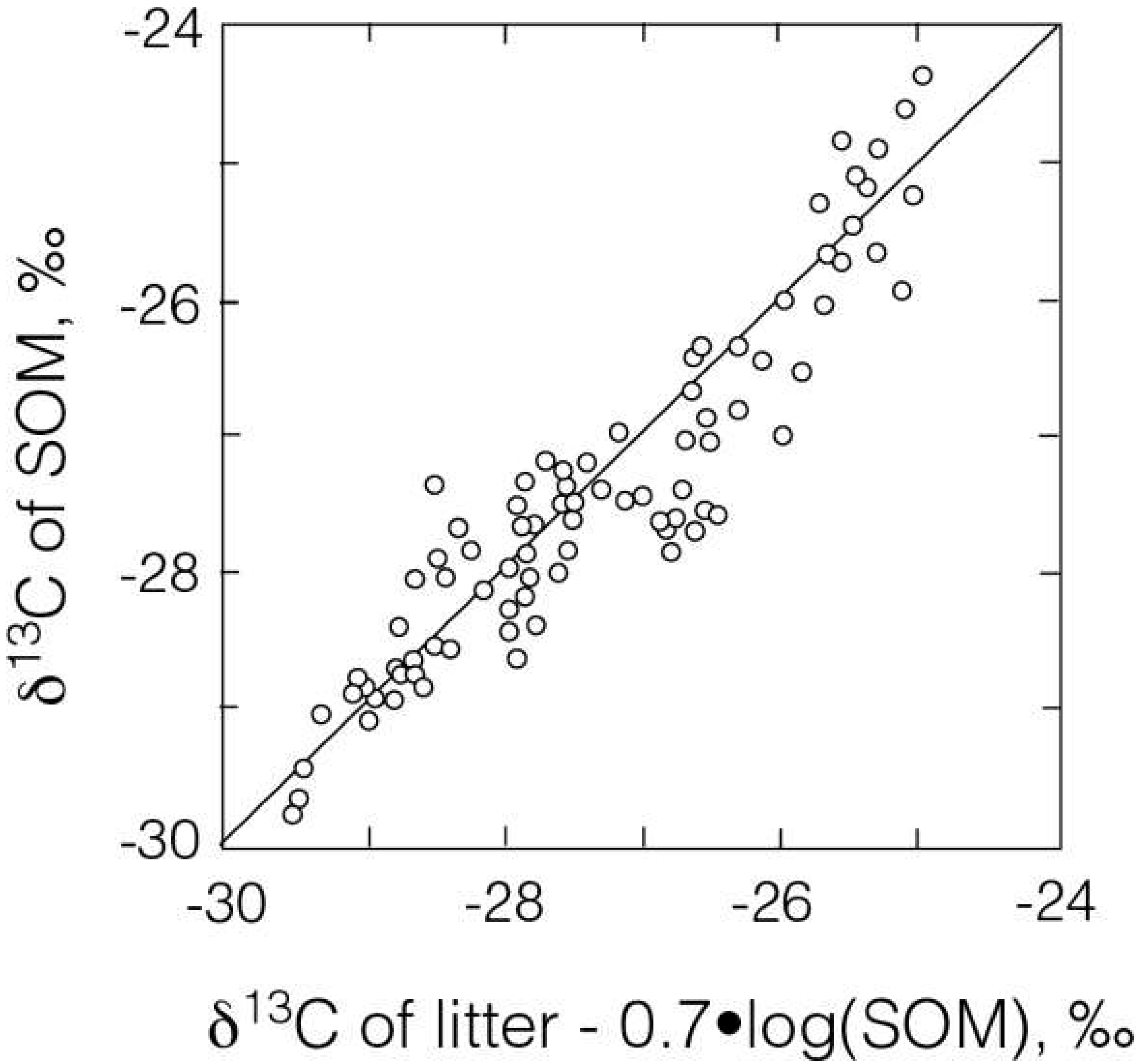
Rochette and Flanagan

Soil CO_2 efflux is related to carbon turnover (forest-to-pasture conversion)



Neill et al. (1996)

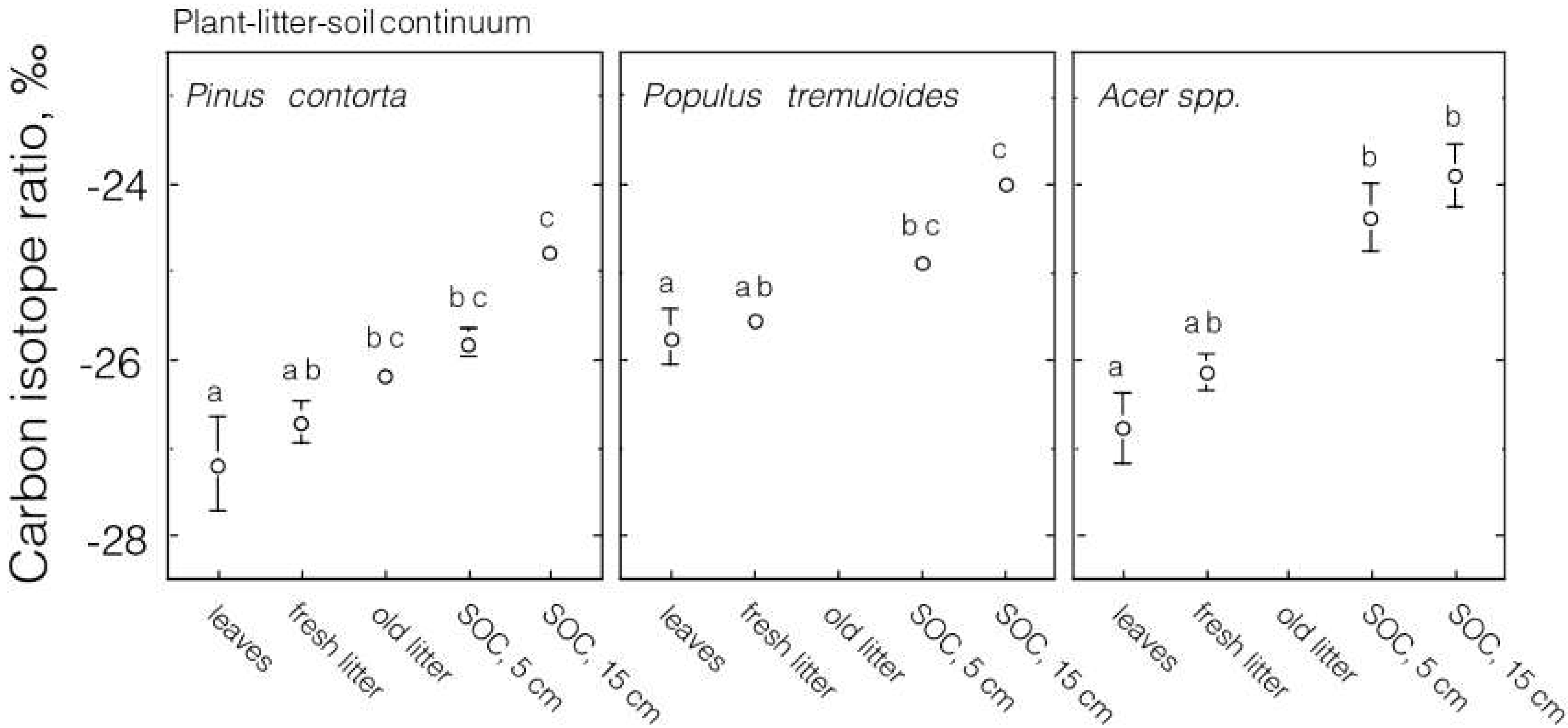
Organic ^{13}C in soils is related to inputs



Balesdent et al. (1993)

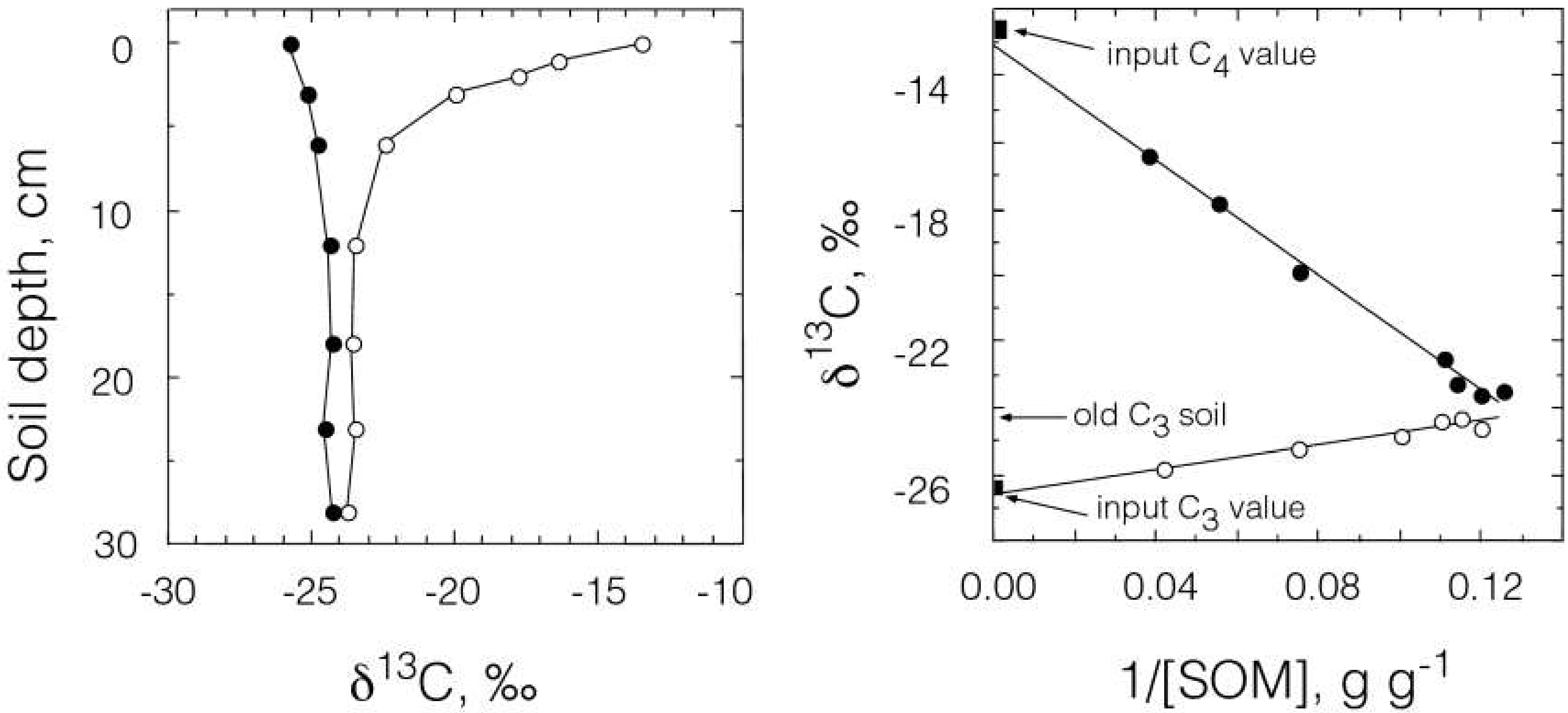
Organic ^{13}C in soils is related to inputs

Note the continuous 13-C enrichment, even though forest type has remained constant



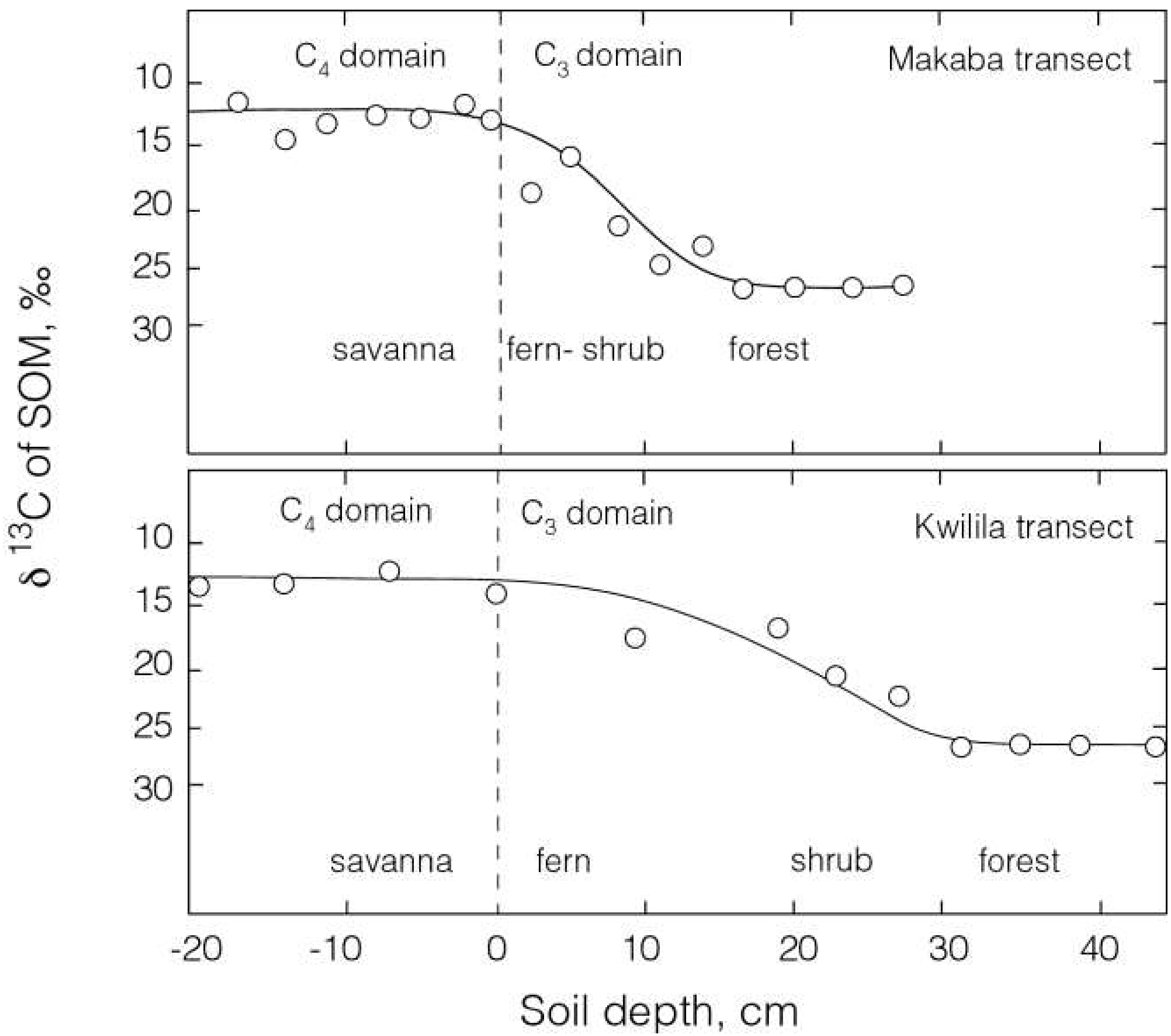
Buchmann et al. (1997)

Organic ^{13}C in soils is related to inputs

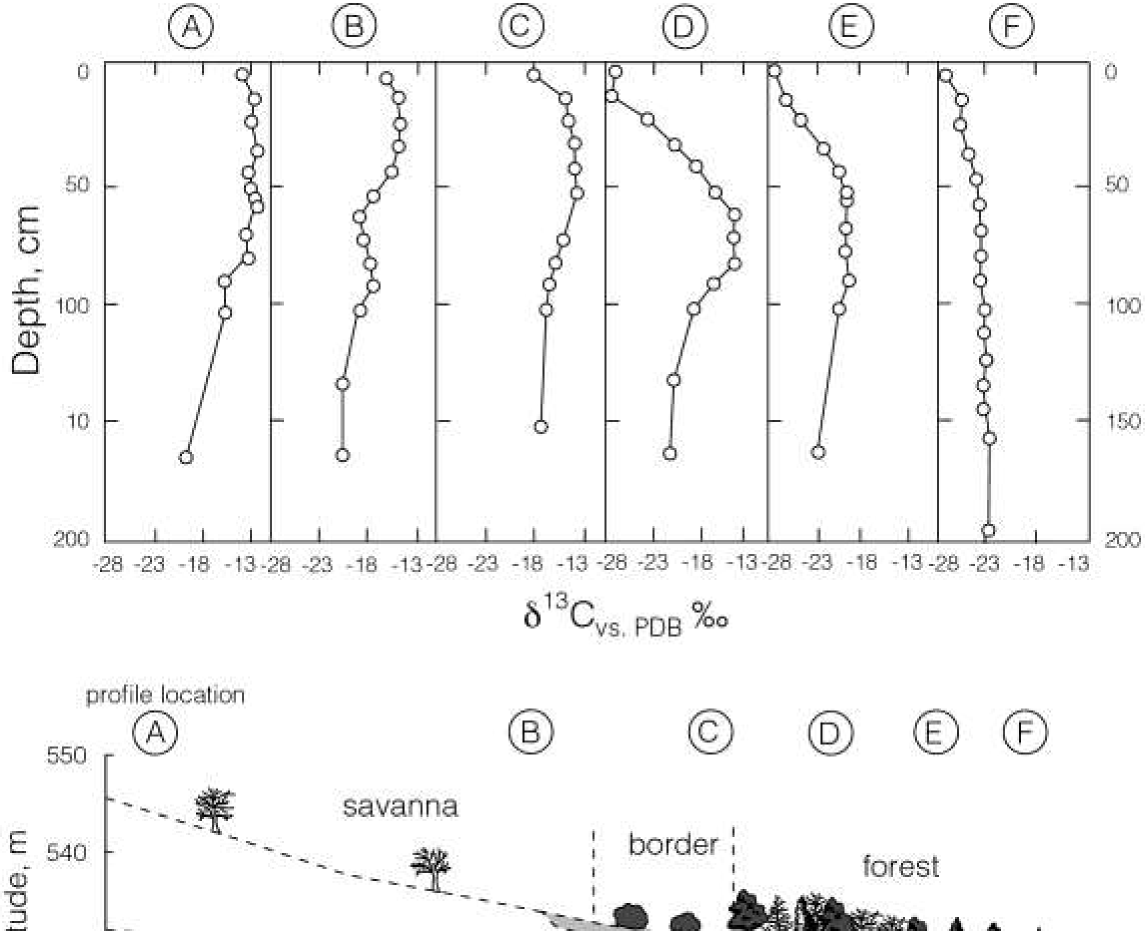


Balesdent and Mariotti (1996)

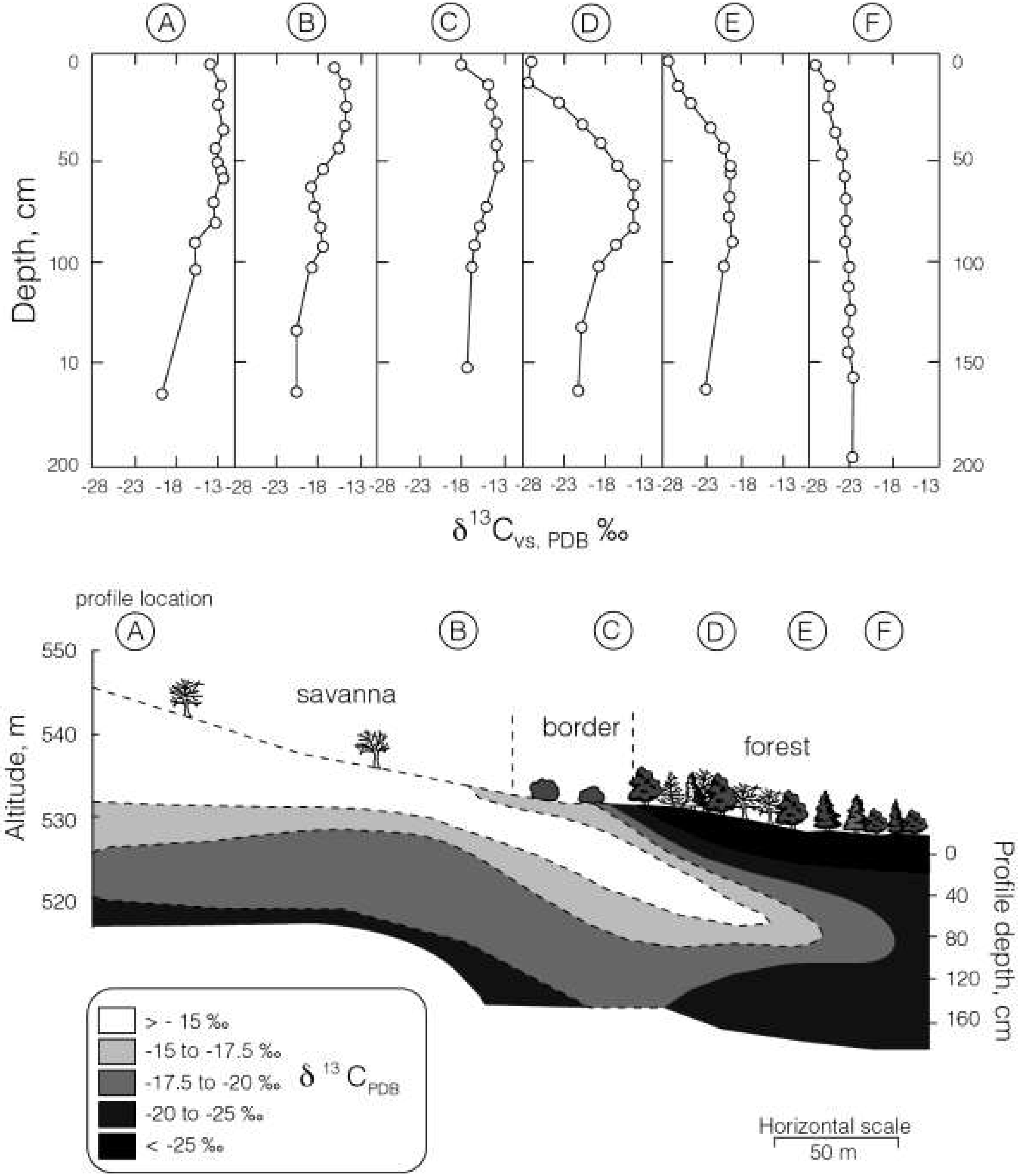
Organic ^{13}C in soils is related to inputs (forest-grassland boundary)



Schwartz et al. (1996)

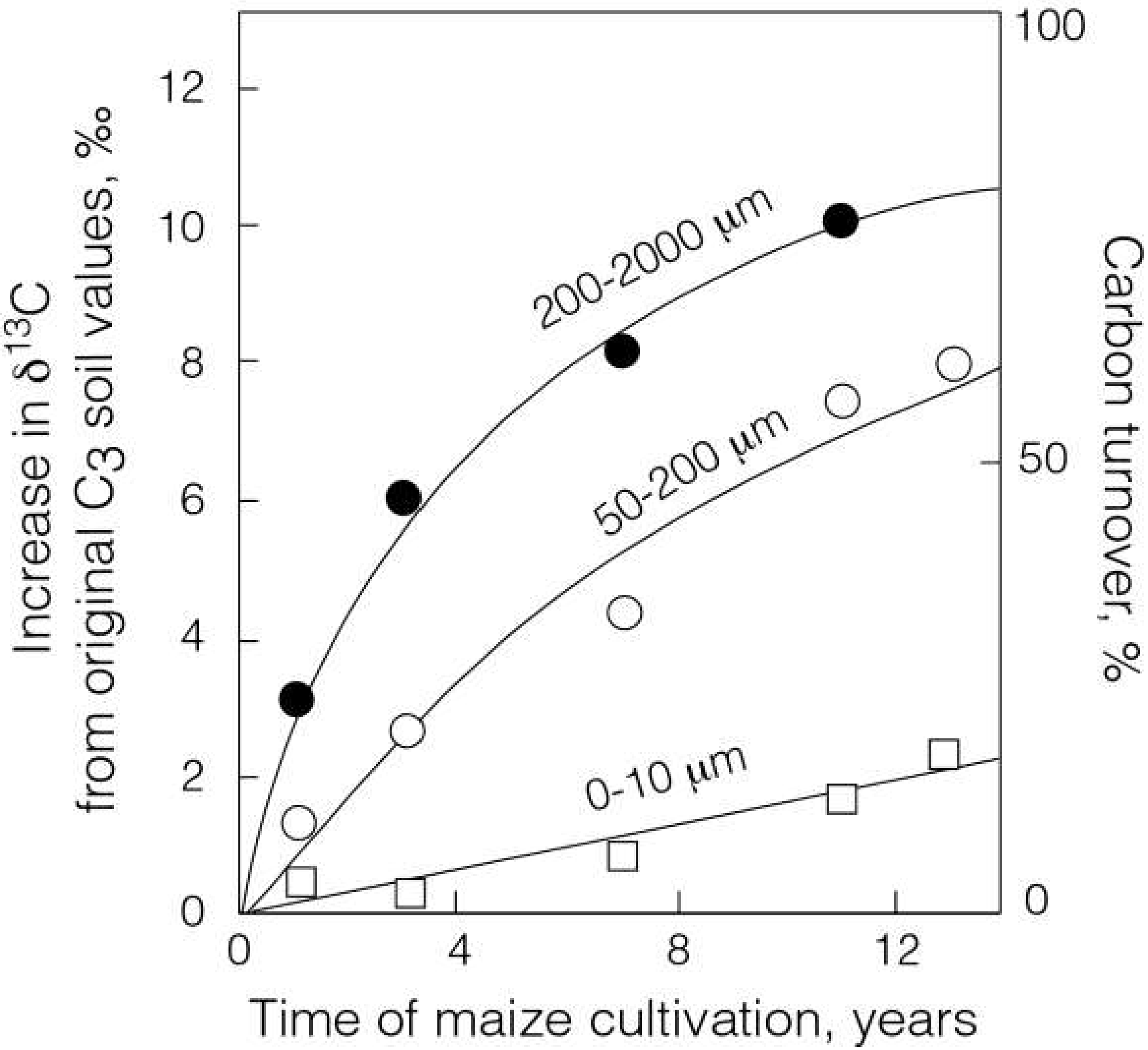


Mariotti and Peterschmidt (1994)

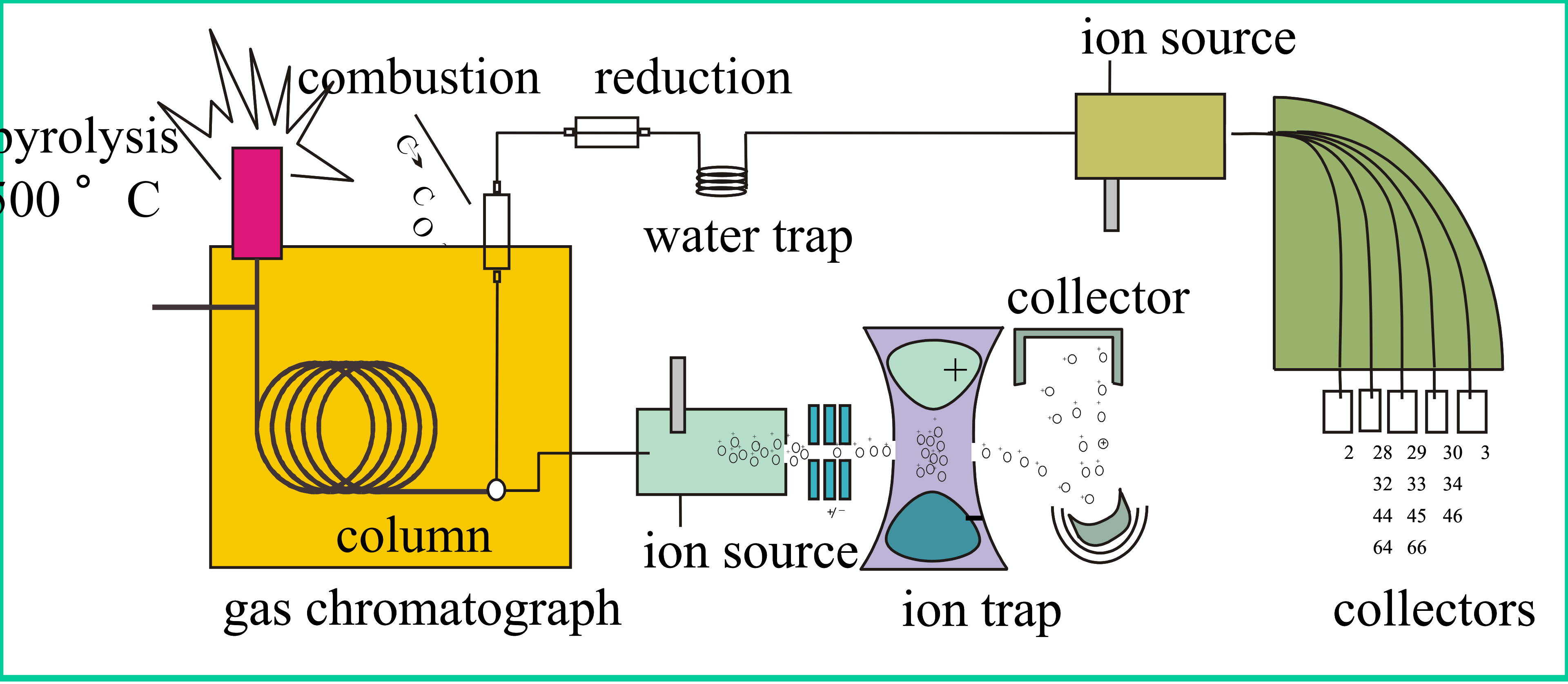


Mariotti and Peterschmidt (1994)

Organic ^{13}C in soils is related to inputs (size dependence of turnover rate)

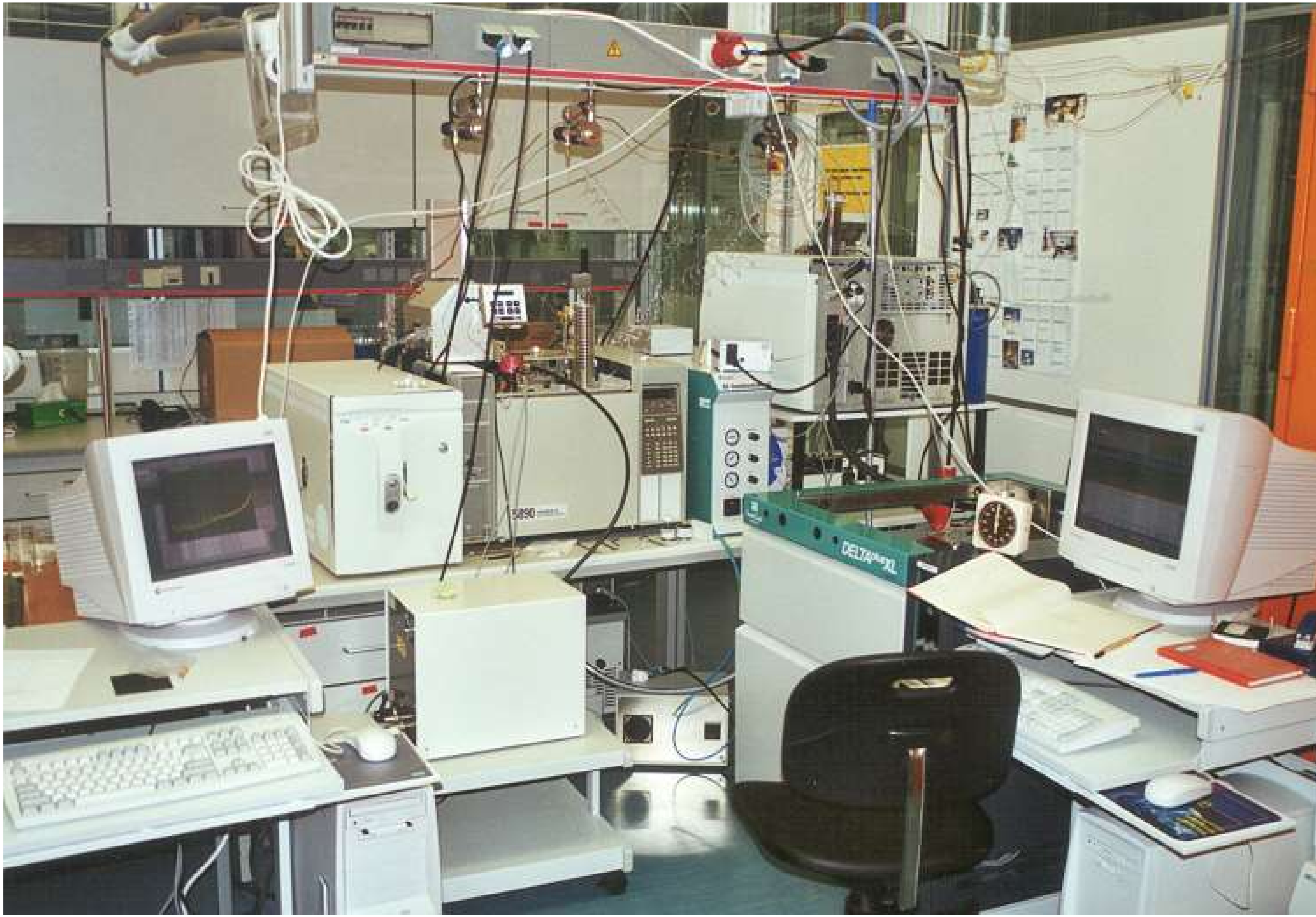


Mariotti and Balesdent (1996)

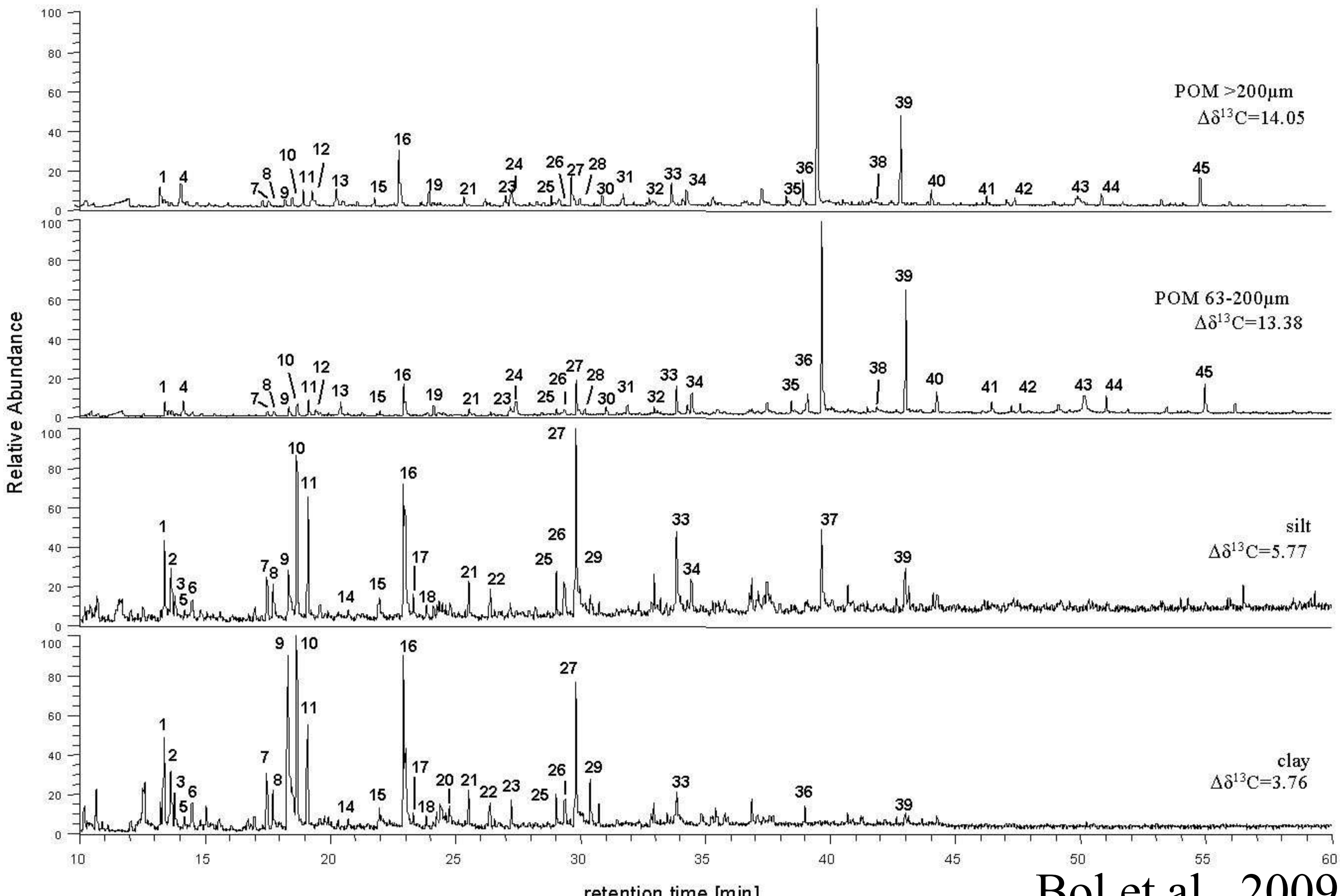


Precursor	Pyrolysis Product
Carbohydrates	Funranes and Pyranes
Protein	Nitriles, Pyrroles and Piperazines
Lignin	Methoxyphenols

after Gleixner et al., 1999

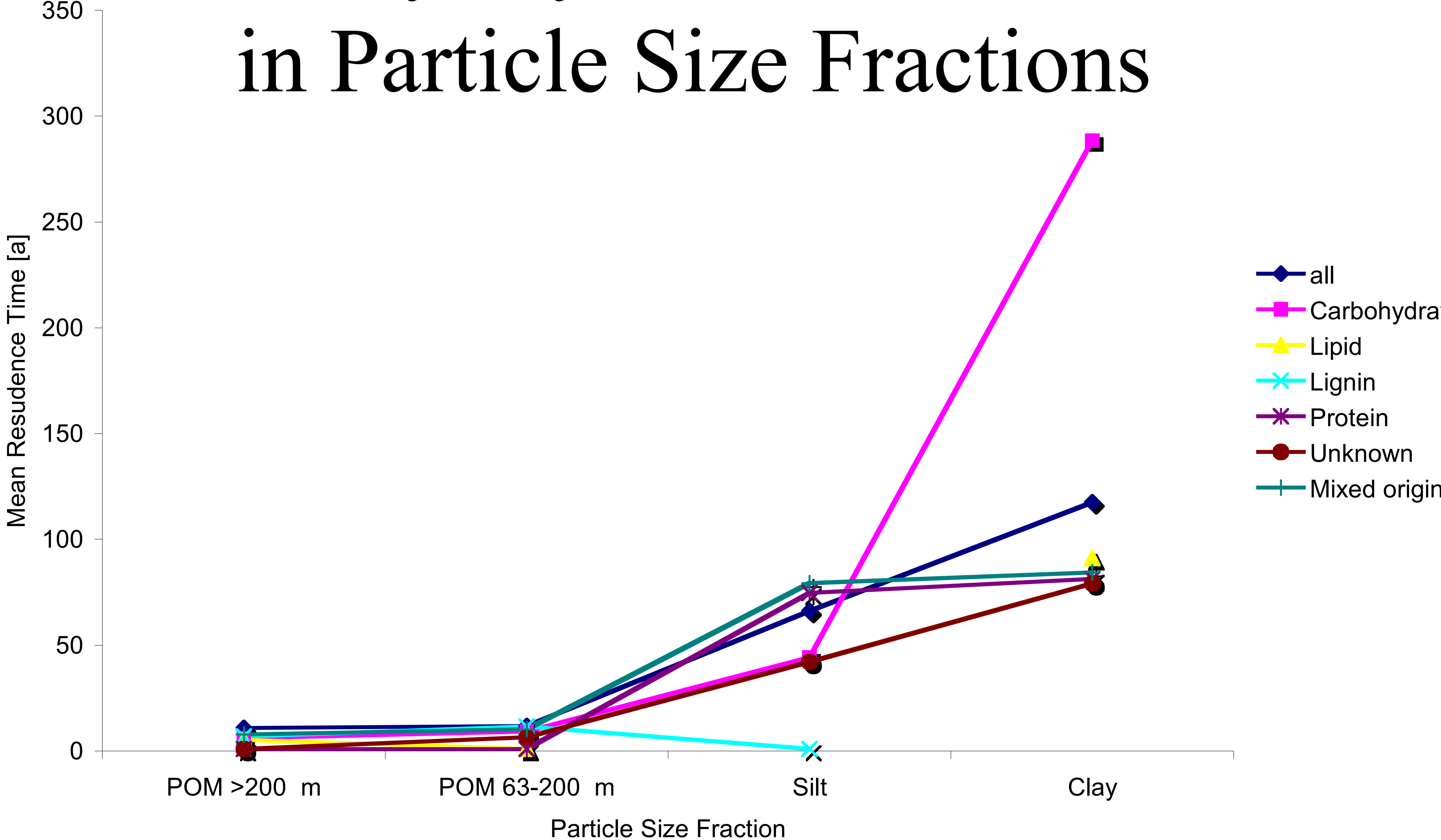

5890
DELTA plus XL

Chemical composition of



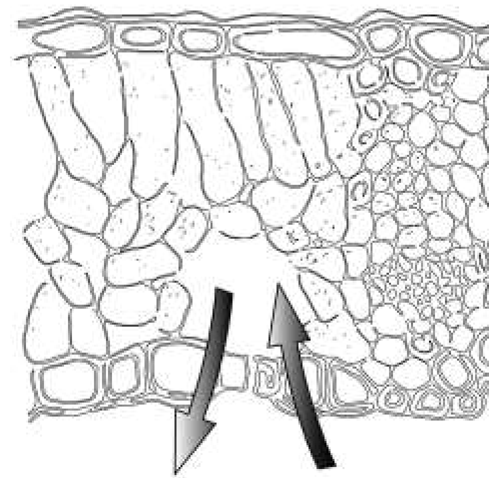
Bol et al., 2009

Mean Residence Time of Pyrolysis Products in Particle Size Fractions



Water-use efficiency is the ratio of assimilation/transpiration (A/E)

$$A = (c_a - c_i)\frac{g}{1.6}$$



$$E = vg$$

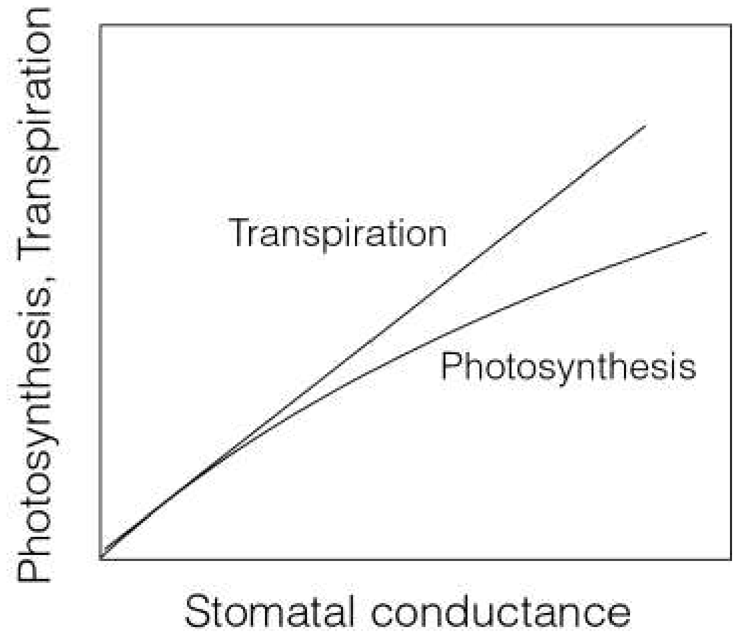
$$\frac{A}{E} = \frac{(c_a - c_i)}{1.6\nu} = \frac{c_a\left(1 - \frac{c_i}{c_a}\right)}{1.6\nu}$$

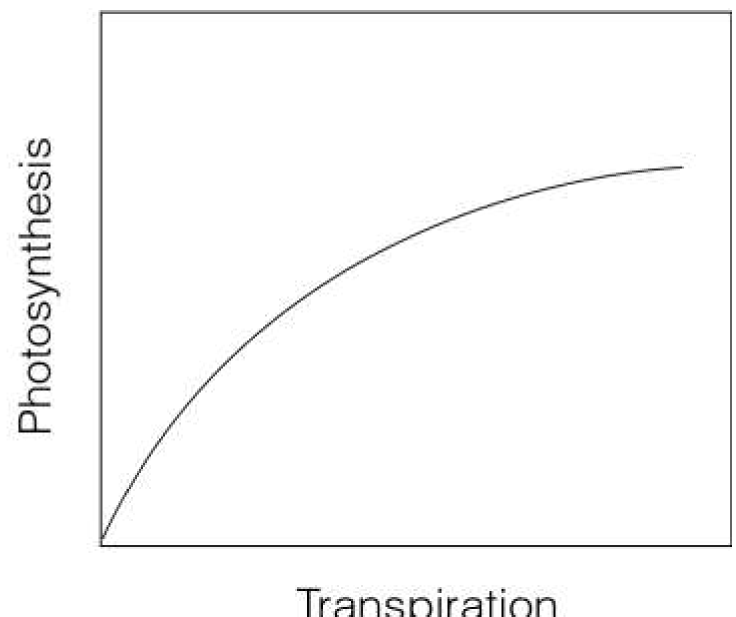
Whole-plant water-use efficiency corrects for respiratory C losses and nonstomatal H_2O losses

$$\frac{A}{E} = \frac{(c_a - c_i)}{1.6\nu} = \frac{c_a\left(1 - \frac{c_i}{c_a}\right)}{1.6\nu}$$

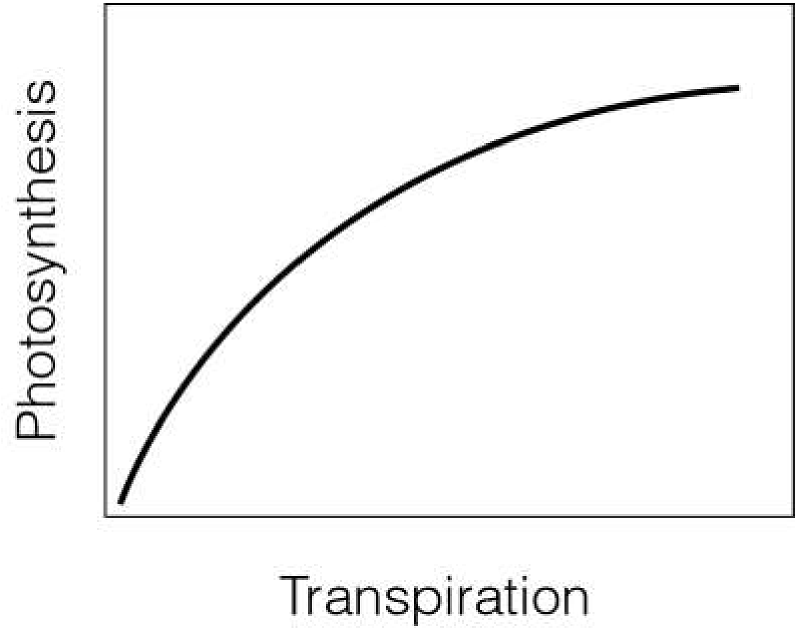
$$W = \frac{c_a\left(1 - \frac{c_i}{c_a}\right)}{1.6\nu} * \frac{(1 - \phi_c)}{(1 + \phi_w)}$$

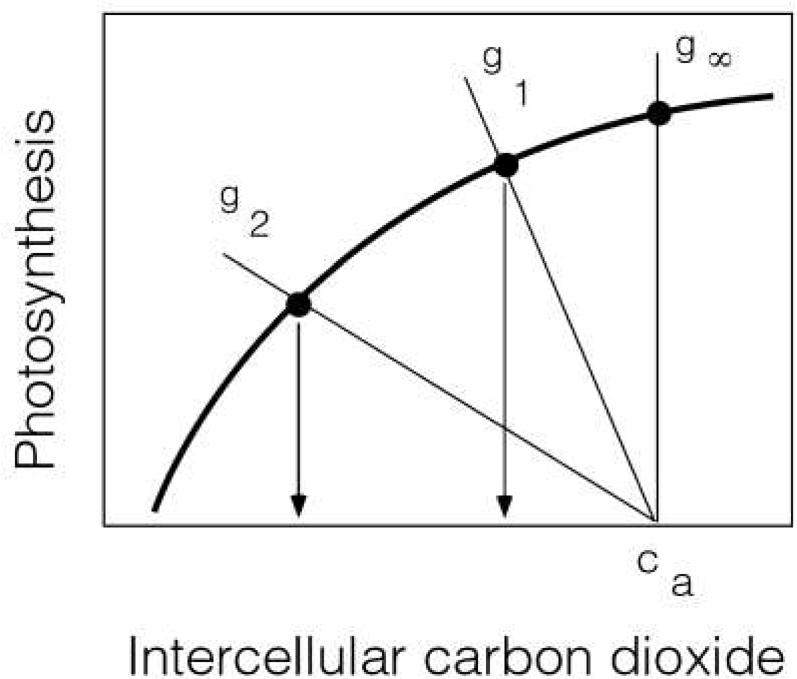
Photosynthesis and transpiration respond to stomatal conductance





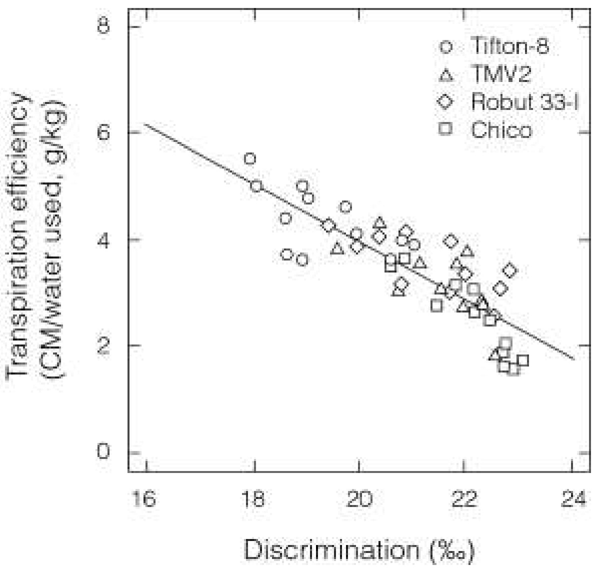
C_3 photosynthesis is nonlinearly related to internal CO_2 levels



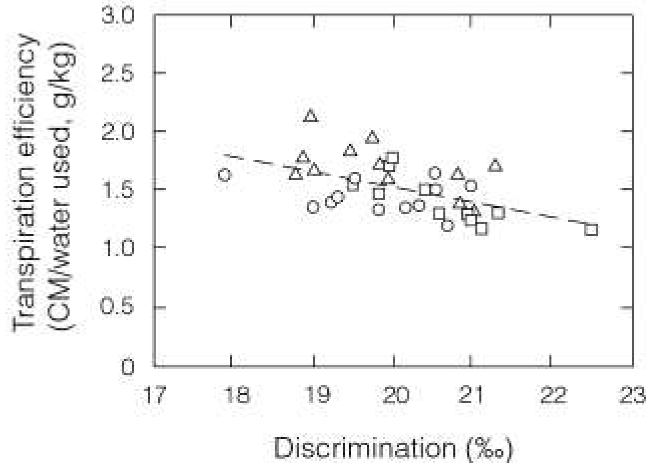


Water-use efficiency is related to ^{13}C discrimination

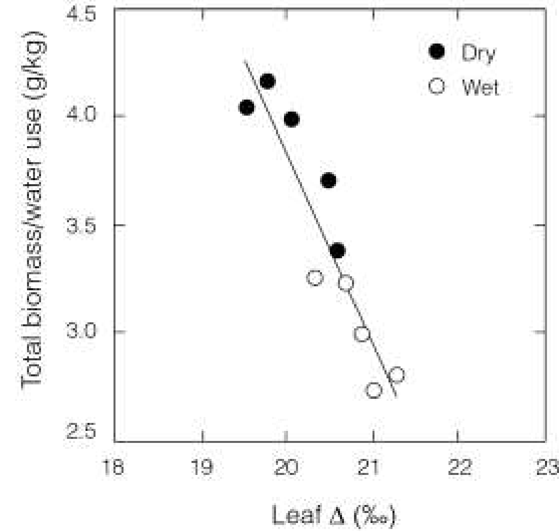
peanut

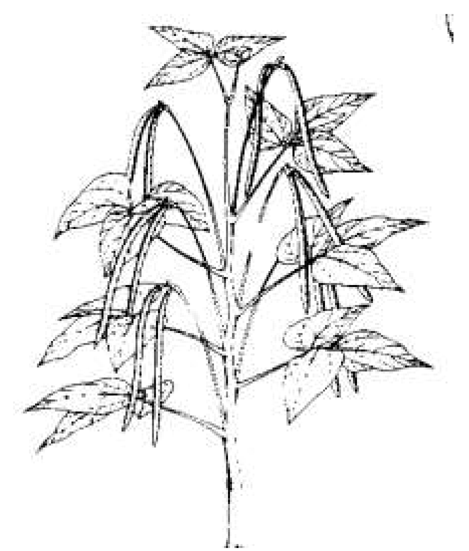


Eucalyptus



cowpea

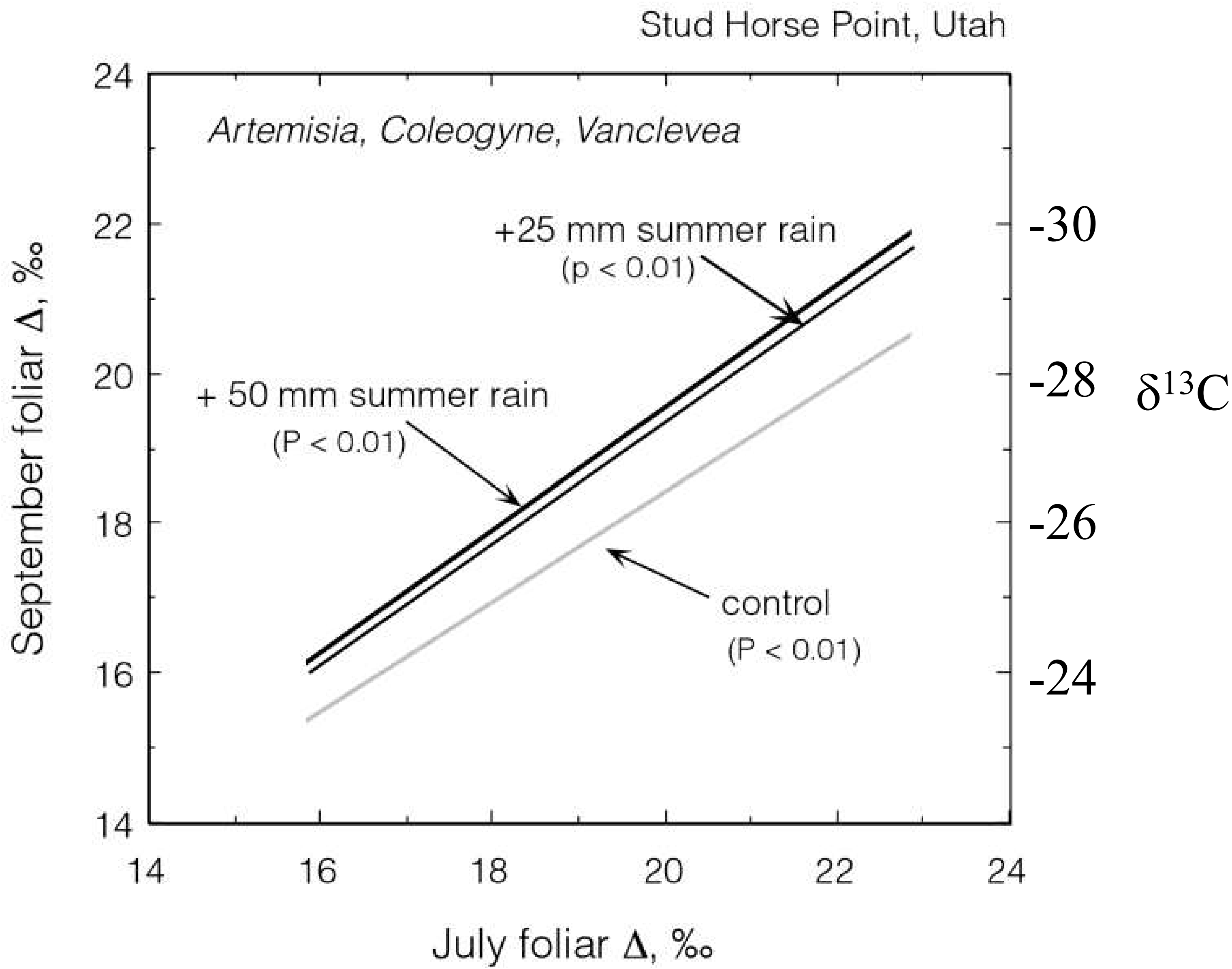




Genetic variation in ^{13}C exists and appears correlated with

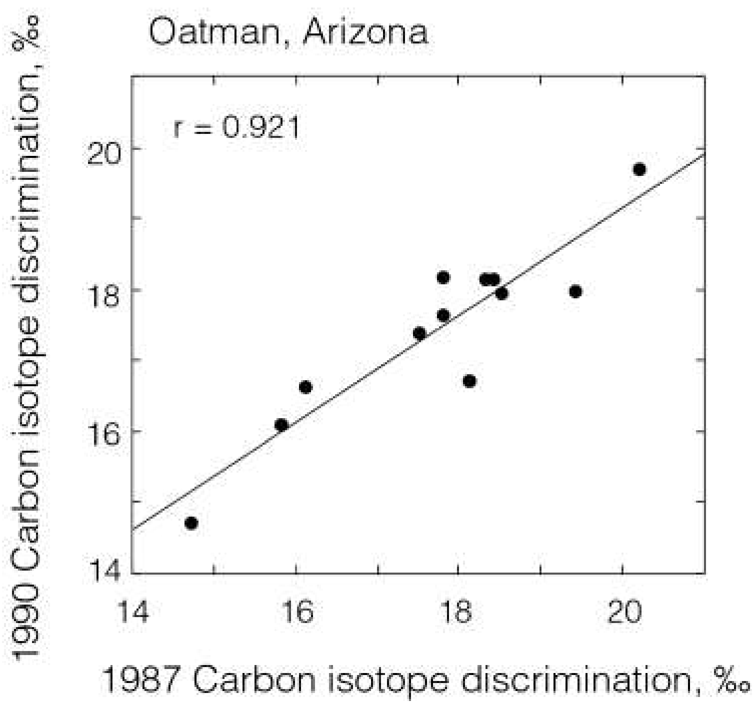
- sensitivity to drought
- maturity date
- life expectancy
- biomass and growth rate
- leaf conductance

There is acclimation to growth environment, but rankings among genotypes remain fixed.

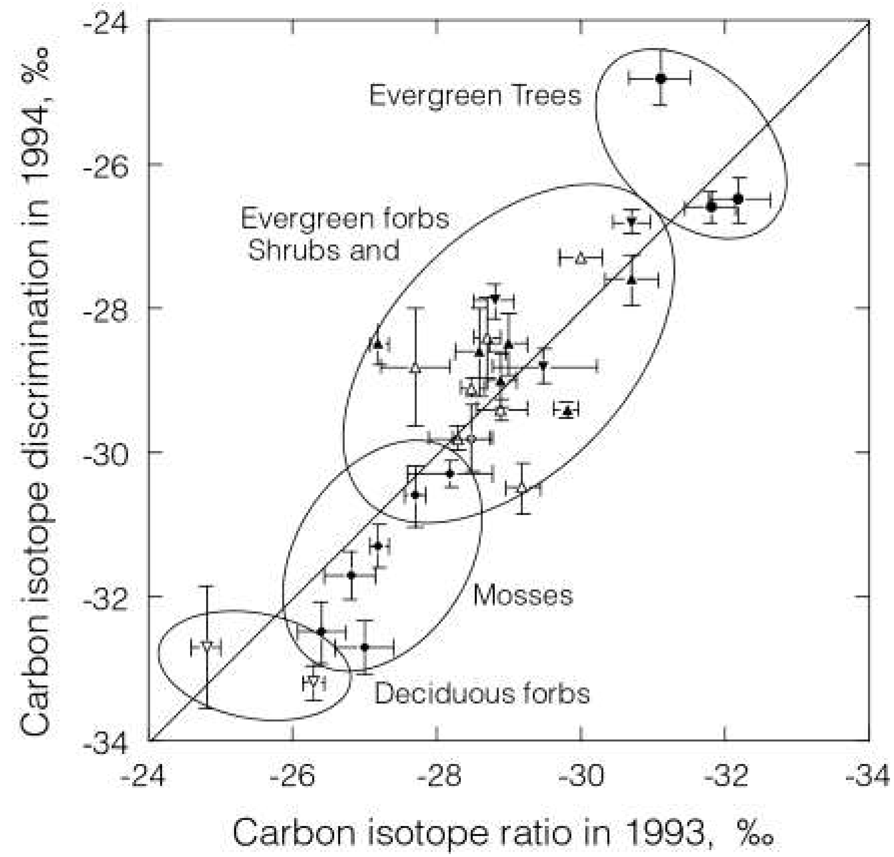


There is acclimation to growth environment, but rankings among genotypes remain fixed.

desert

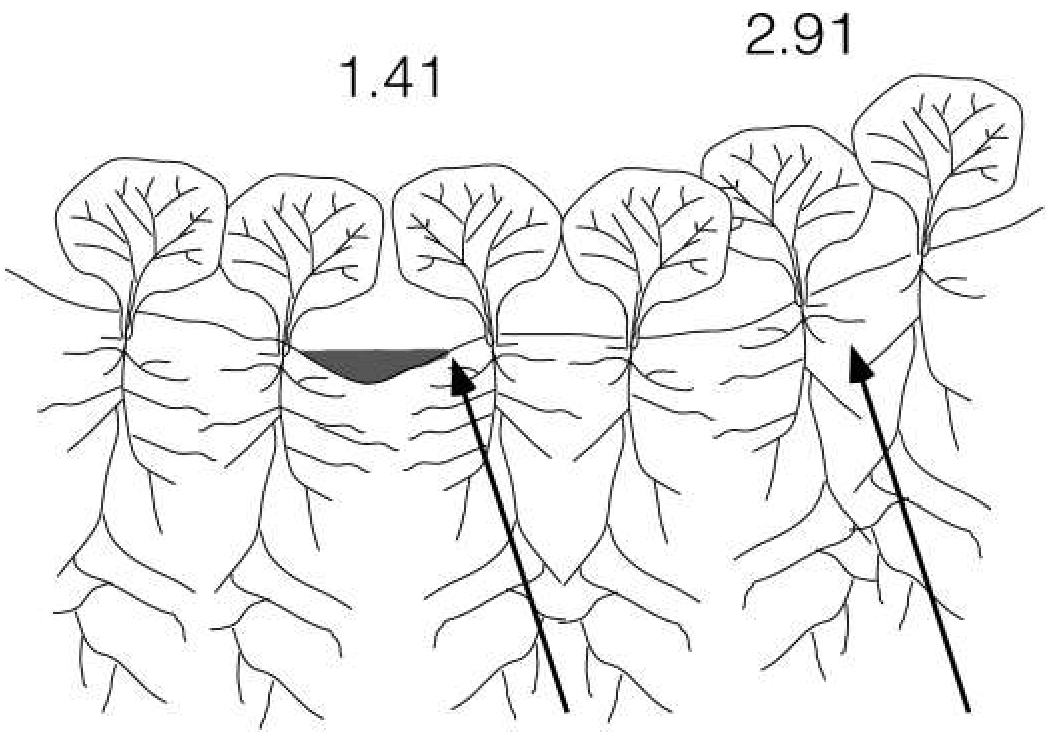


boreal forest



Boxelder (*Acer negundo*)

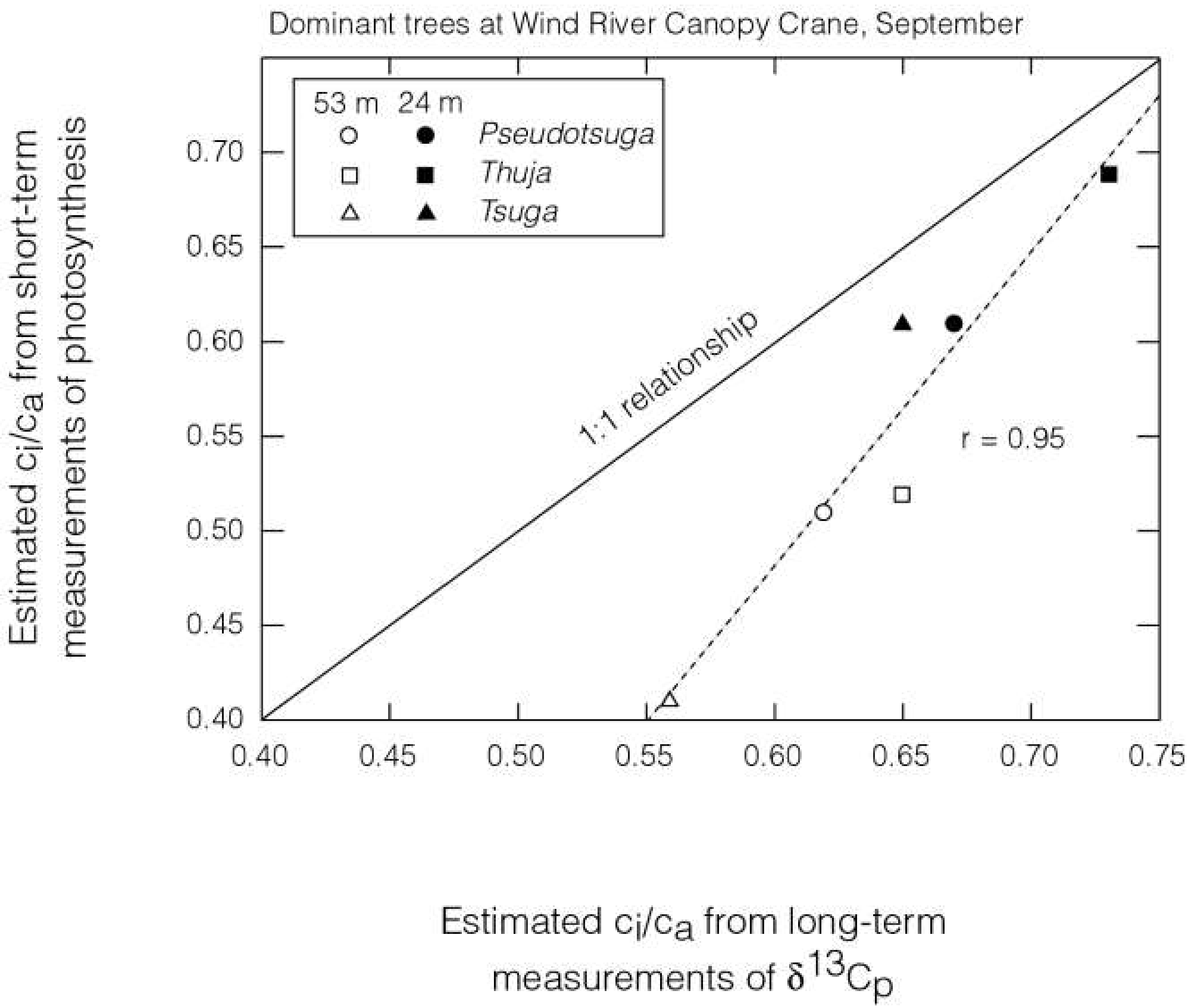
sex ratio (male/female)



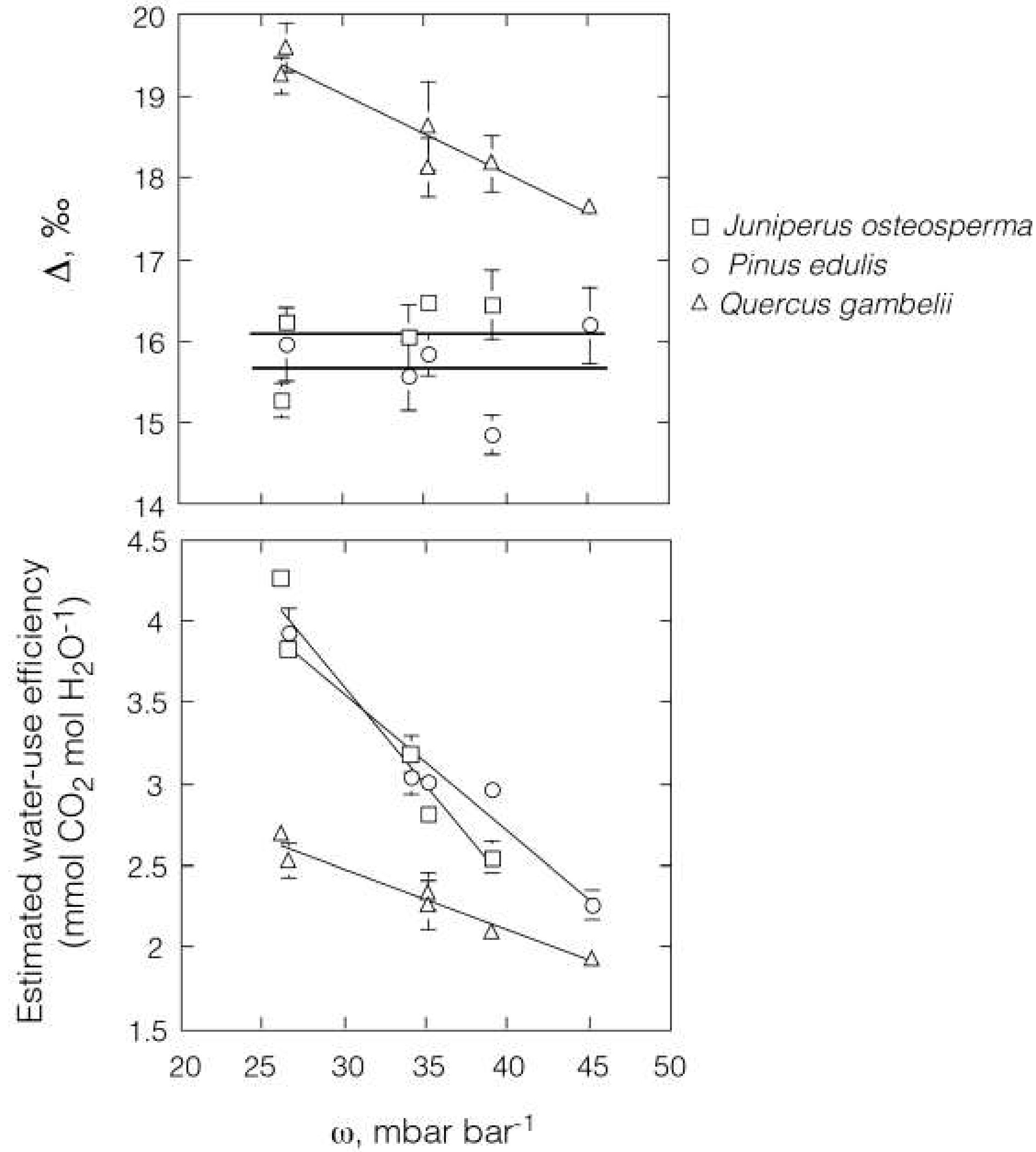
carbon isotope ratio	male	female
Box 1	-28.0 ‰	-29.5 ‰
Box 2	-26.6 ‰	-29.5 ‰

Dawson and Ehleringer (1993)

The ^{13}C values of organic tissues and gas fluxes can differ because of short-term carbon dynamics

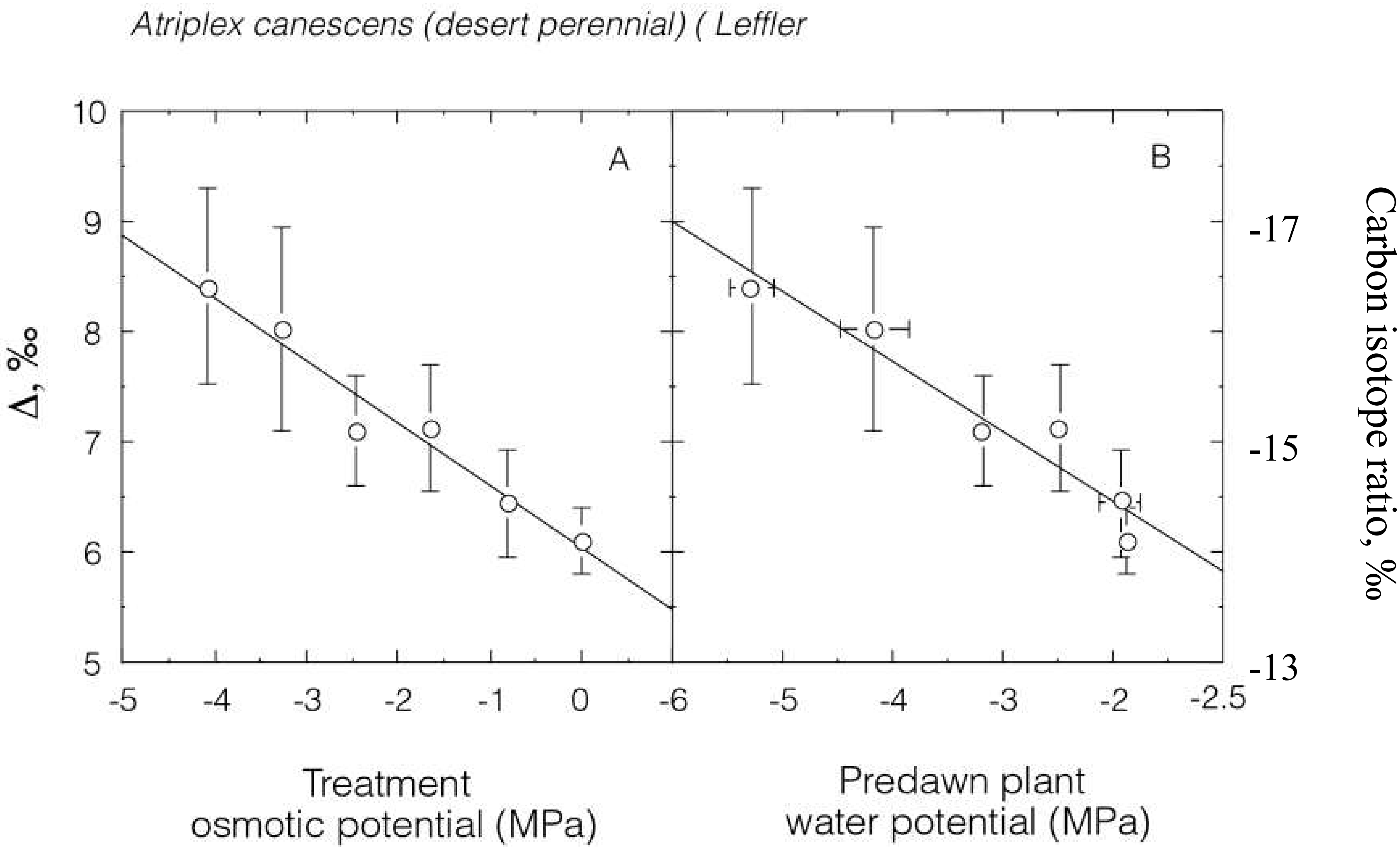


C_3 carbon isotope discrimination decreases with increased aridity



Williams and Ehleringer (1998)

C_4 carbon isotope discrimination increases with increased aridity



Leffler and Ehleringer (unpubl)