Concepts and constraints for scaling from baseline metabolism to ecosystem carbon relations

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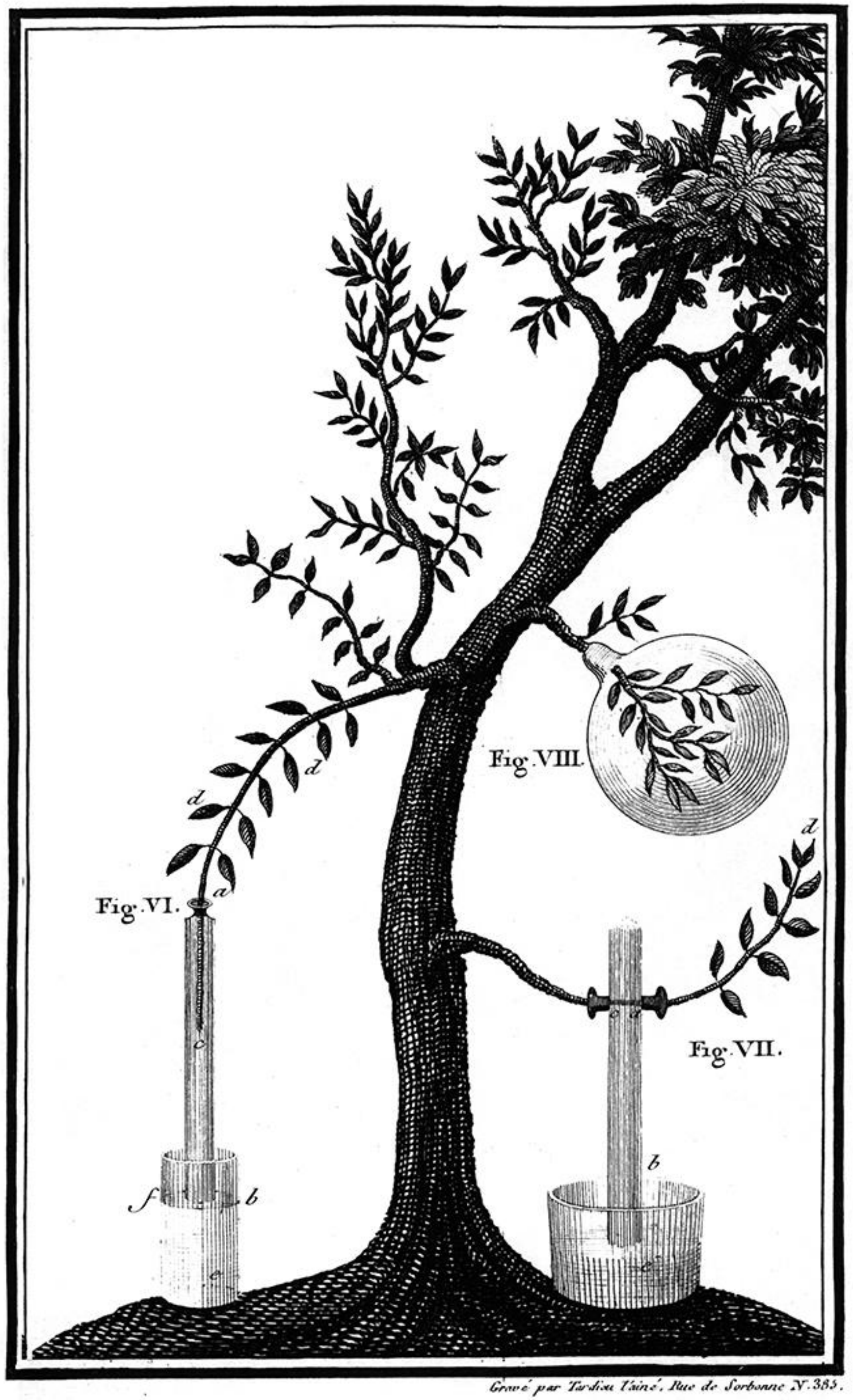
In Geneva 200 years ago:

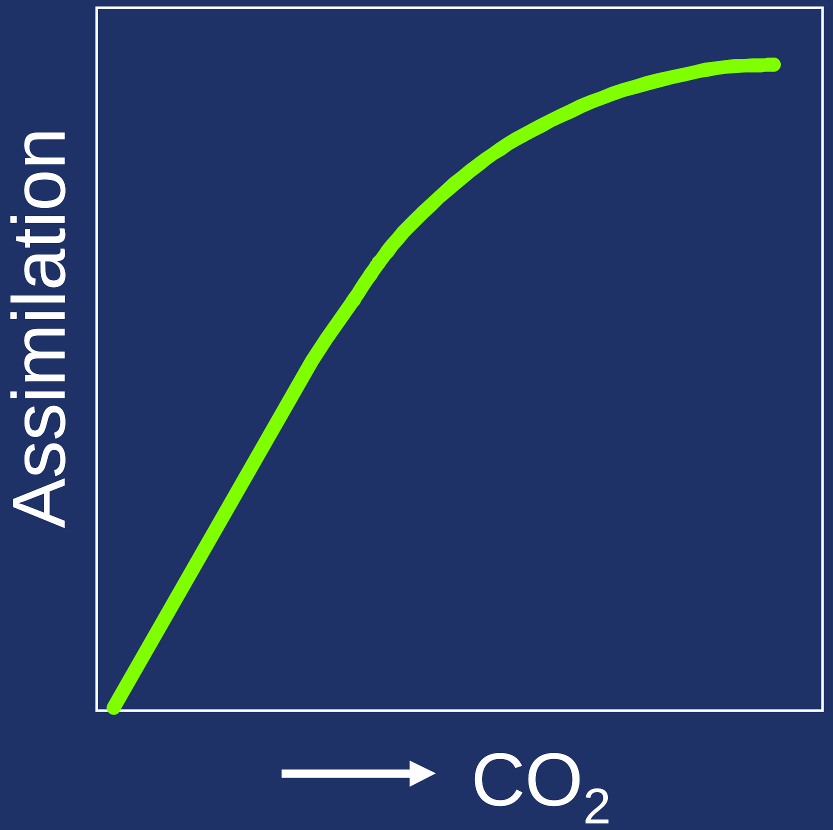
‘The primary plant food comes from air‘

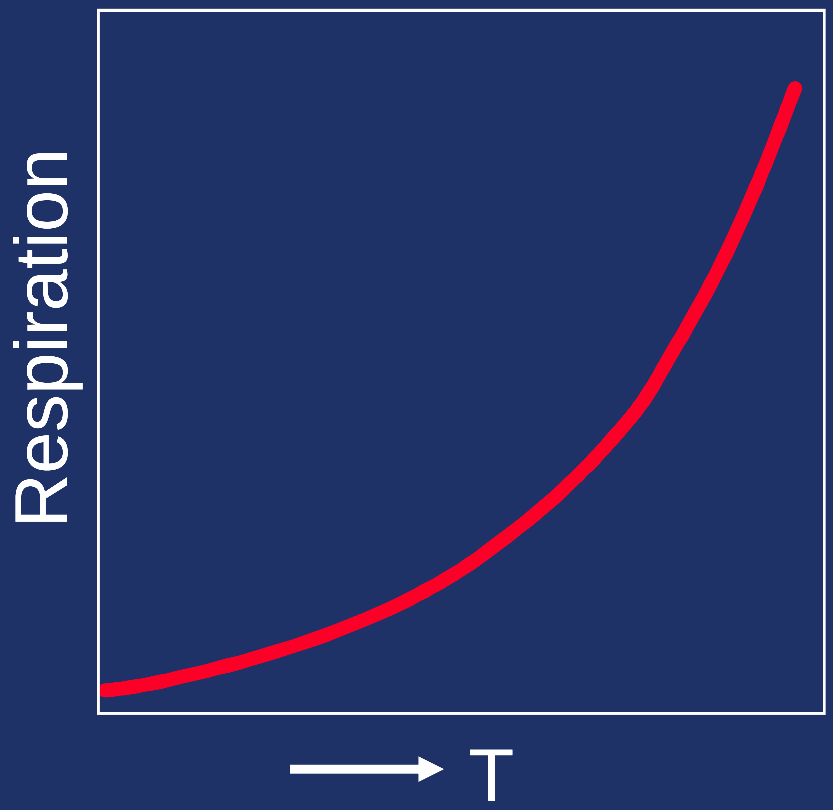
Nicolas-Théodore de Saussure (1804)
Recherches chimiques sur la Végétation.
Paris.



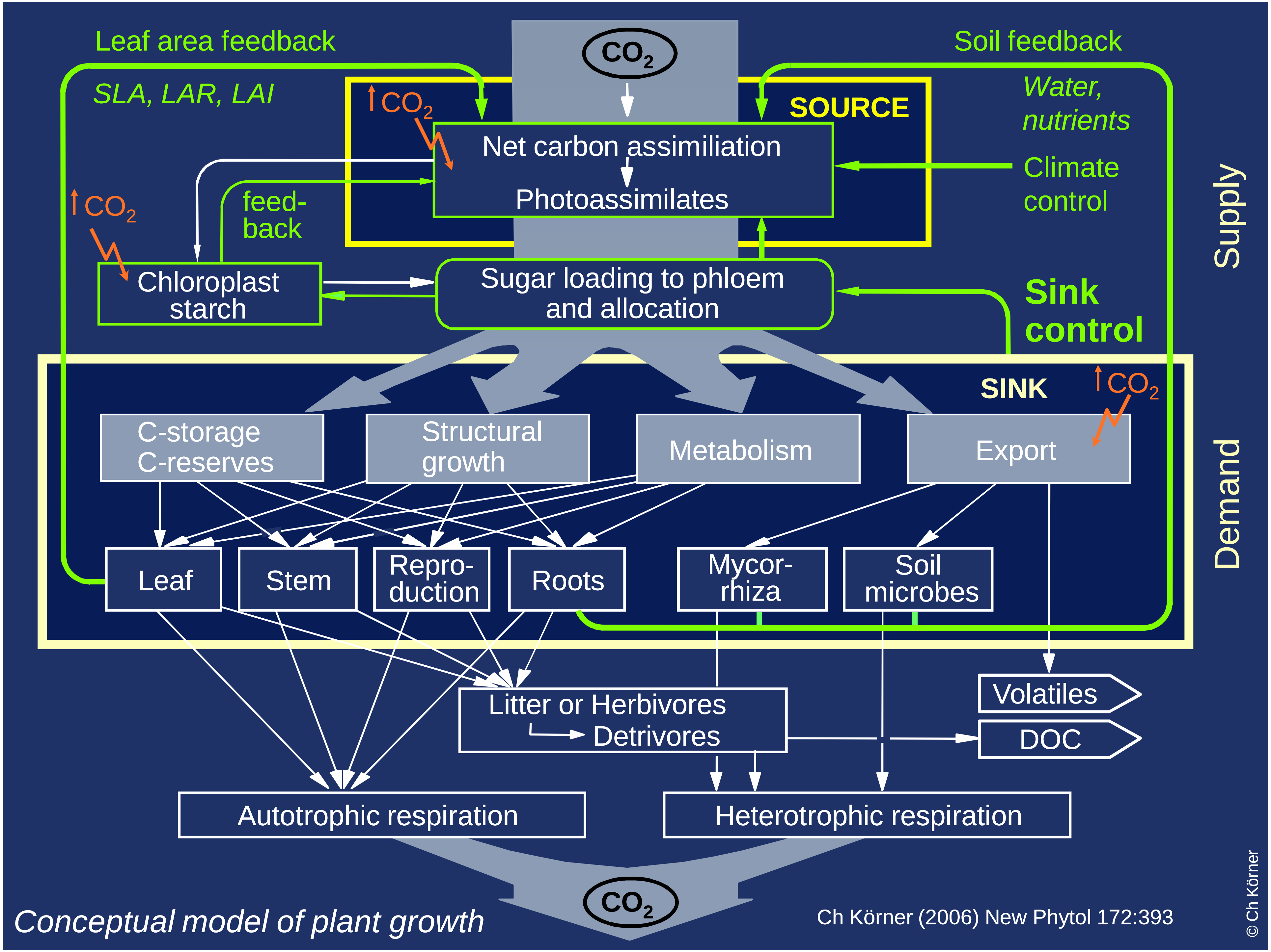
The new way.....

Are these basic physiological functions drivers or driven?





driven by what?



CO_2
Leaf area feedback
SLA, LAR, LAI
Soil feedback
Water, nutrients
SOURCE
↑CO_2
Net carbon assimiliation
Photoassimilates
Climate control
↑CO_2
feed-back
Chloroplast starch
Sugar loading to phloem and allocation
Sink control
Supply
SINK
↑CO_2
C-storage C-reserves
Structural growth
Metabolism
Export
Demand
Leaf
Stem
Repro-duction
Roots
Mycor-rhiza
Soil microbes
Volatiles
Litter or Herbivores
Detrivores
DOC
Autotrophic respiration
Heterotrophic respiration
CO_2
Conceptual model of plant growth
Ch Körner (2006) New Phytol 172:393
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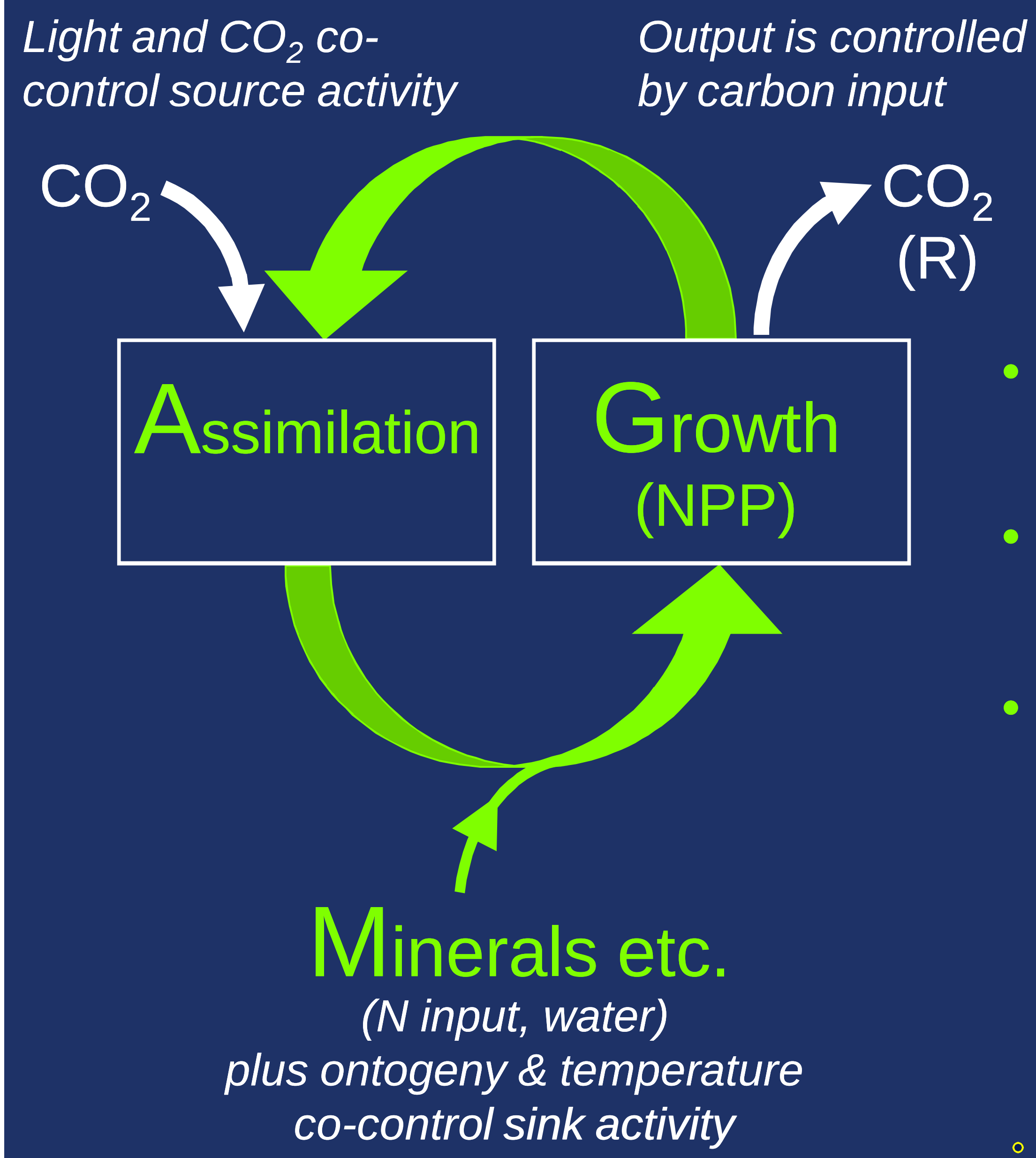
Assimilation drives growth or *vice versa*?

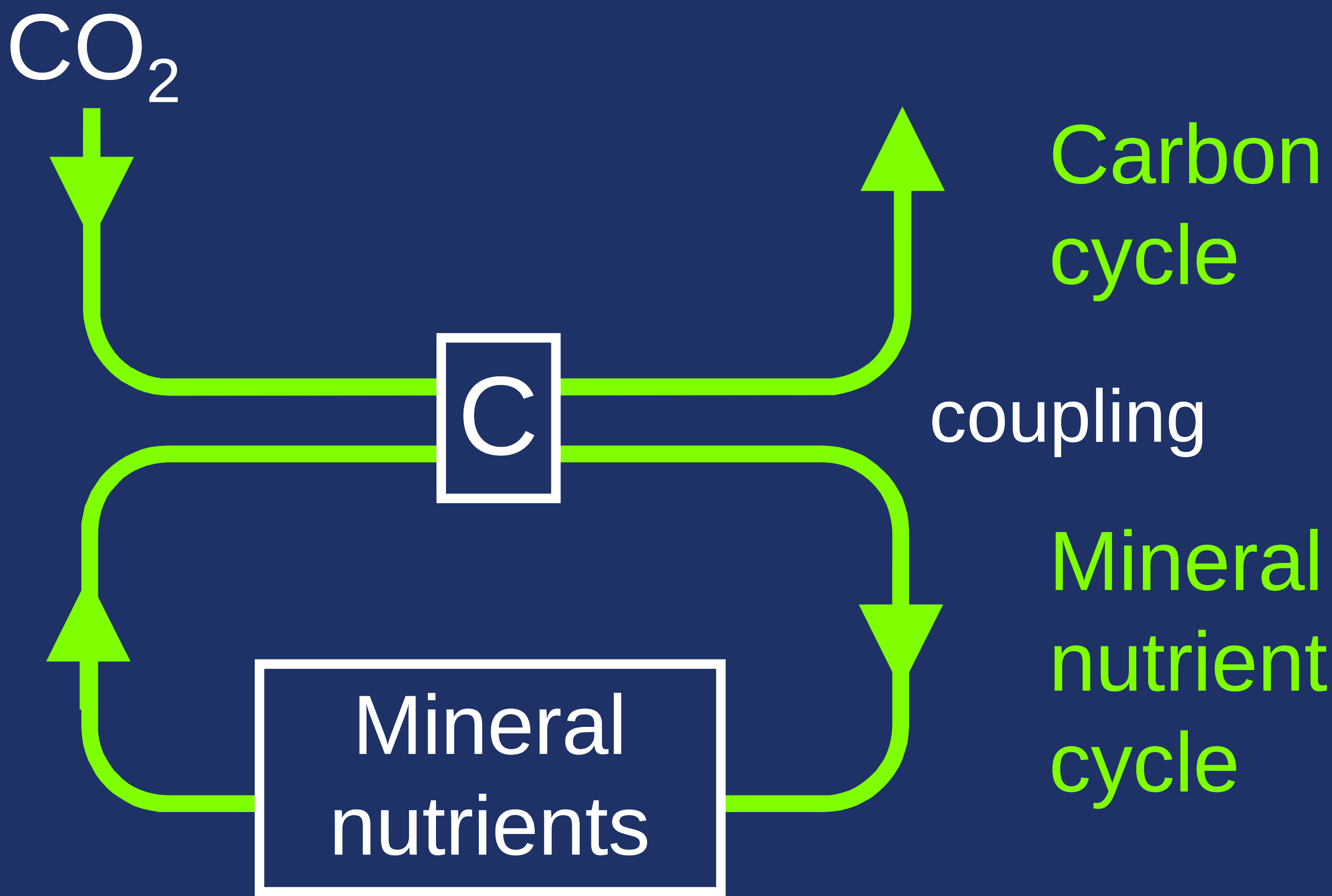


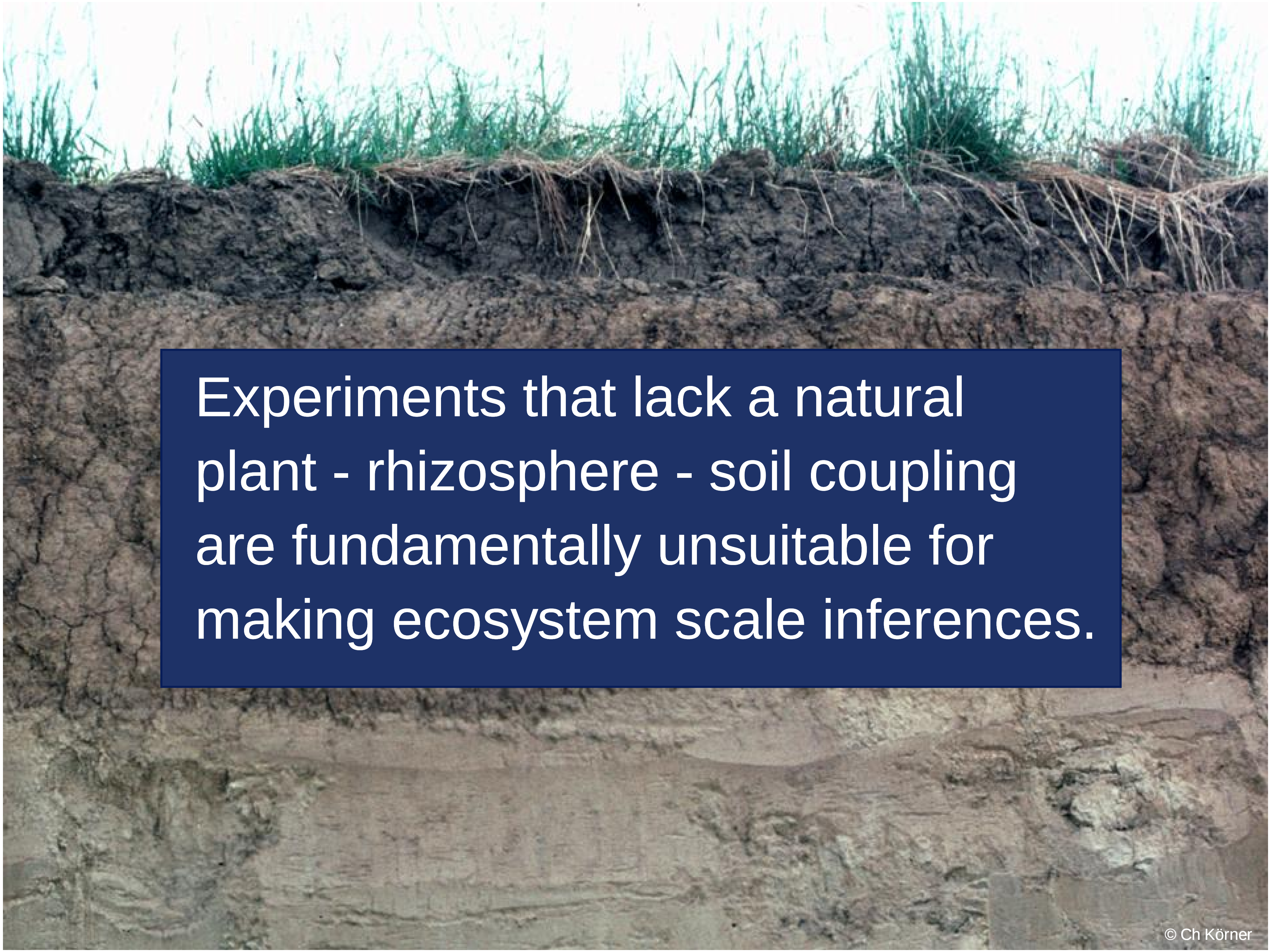
A or G first?

- Whenever M is limiting, G controls A
- Whenever CO_2 or light are limiting, A controls G
- The A ⟷ G fine tuning is masking cause and consequence
  → manipulative experiments

chicken or egg first?

The ecosystem carbon cycle is driven by the nutrient cycle and other growth ‘facilitators‘




Experiments that lack a natural plant - rhizosphere - soil coupling are fundamentally unsuitable for making ecosystem scale inferences.
© Ch Körner

Annual ecosystem R is driven by

- demand (autotrophic R; growth, maintenance, nutrient uptake)
- substrate supply (heterotrophic R)
- duration of active period (environmental conditions x time)

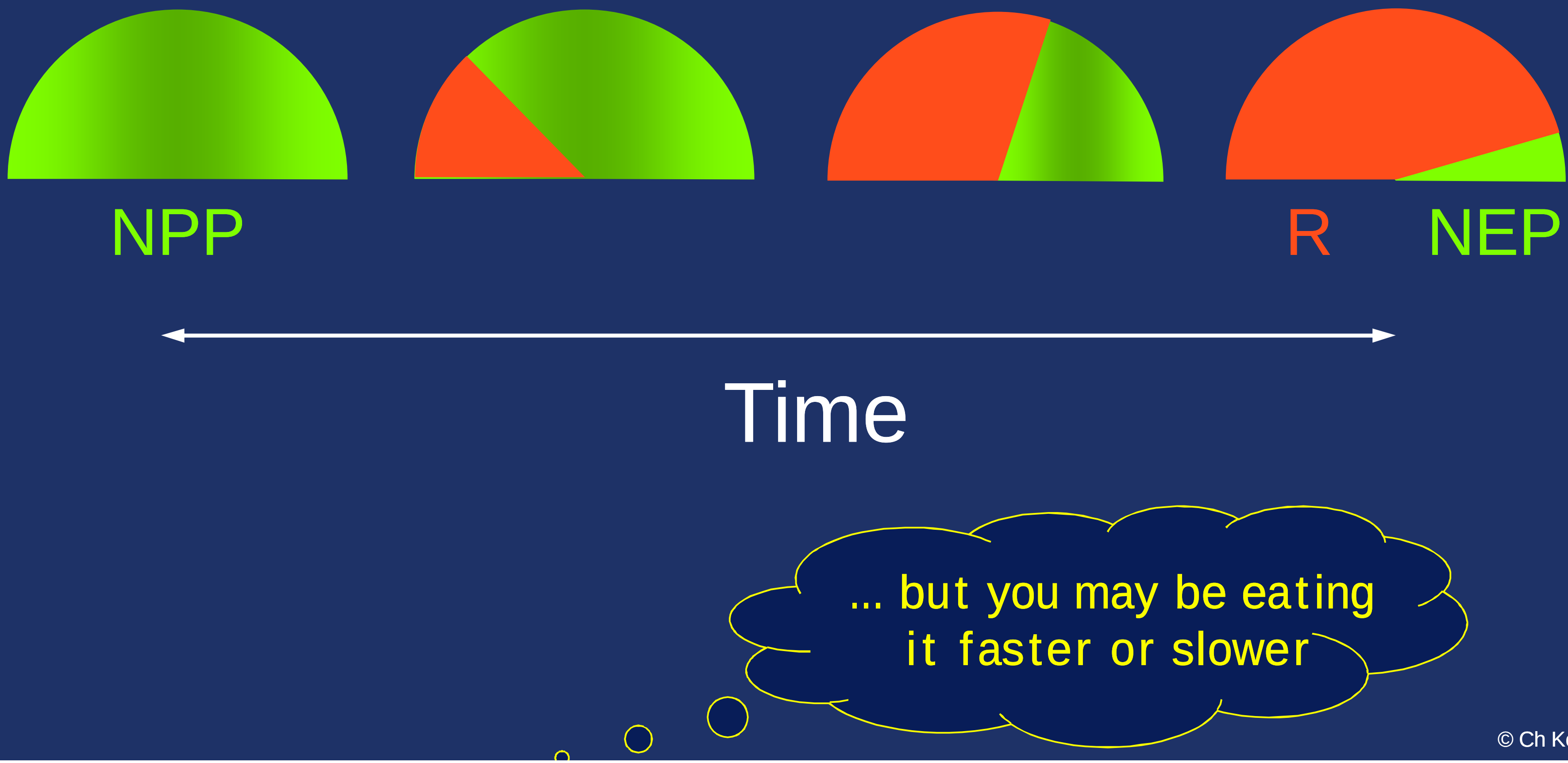
In the long run ...

- R is largely a function of NPP
- NPP = f(soils, age, temperature, etc.)
- R cannot be decoupled from NPP

→ Hence, there is no independent temperature response.

you can eat
the lunch only once

Temporal shifts of R f(T, H_2O) should not be taken as evidence for increased or decreased ΣR



The consequences of climatic warming on soil-CO_2-release:

It is unquestioned that respiratory metabolism, including soil respiration, responds to temperature on an instantaneous, hourly or daily scale.

<u>Hypothesis:</u>

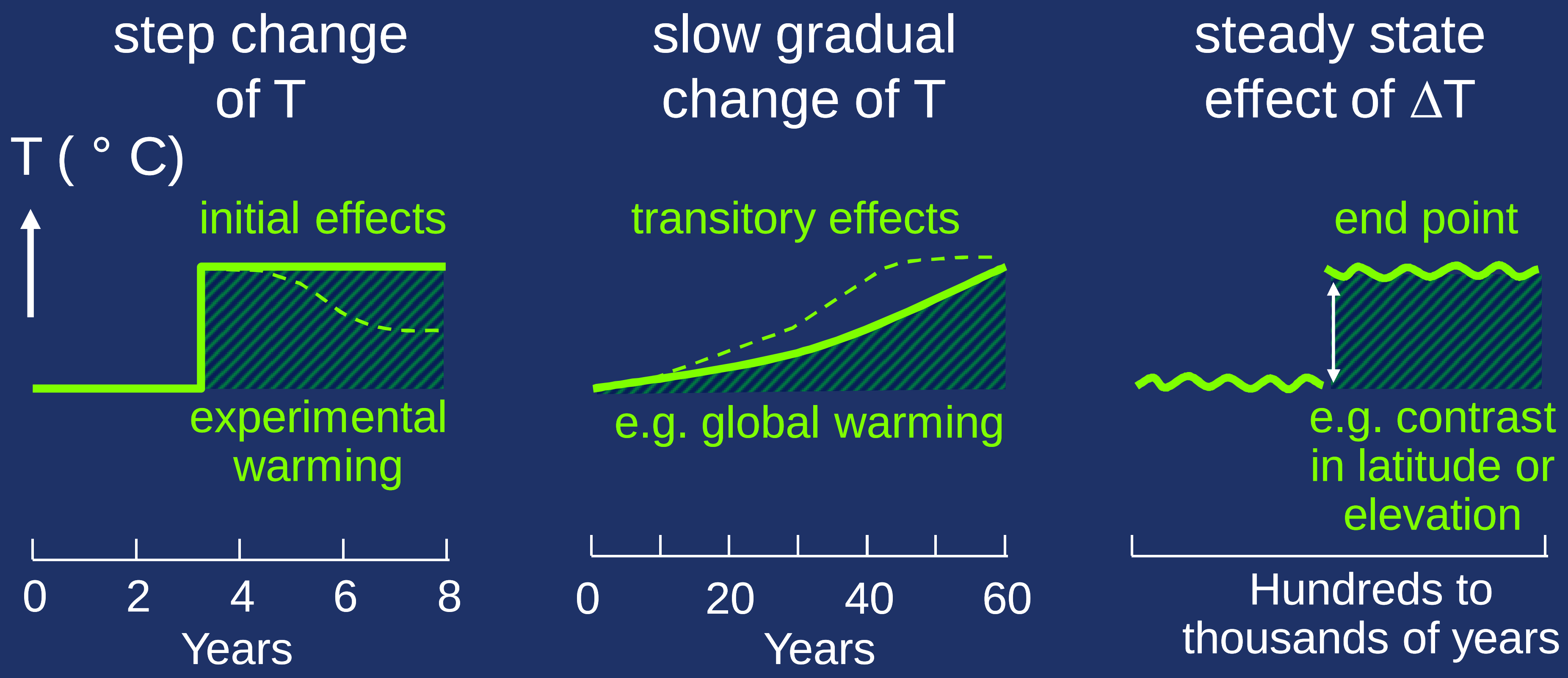
On a full or multi-year scale, soil respiration is a function of NPP, irrespective of temperature.

(Raich JW & Nadelhoffer KJ 1989, Ecology 70:1346
Kuzyakov Y & Gavrichkova O 2010, GCB 16:3386)

In summary,
I suggest a shift in paradigms

sink activity	(demand)	drives A
NPP	(supply)	drives R

Manipulative experiments



unavoidable overestimation → R f(T) Answers ← potential underestimation

How many years does it take to arrive at steady state R?

Results sofar suggest > 5 << 100 years

The challenge:

How can we seperate the intrinsic effect of rising temperature on R_s from the NPP-only driven effect on R_s?

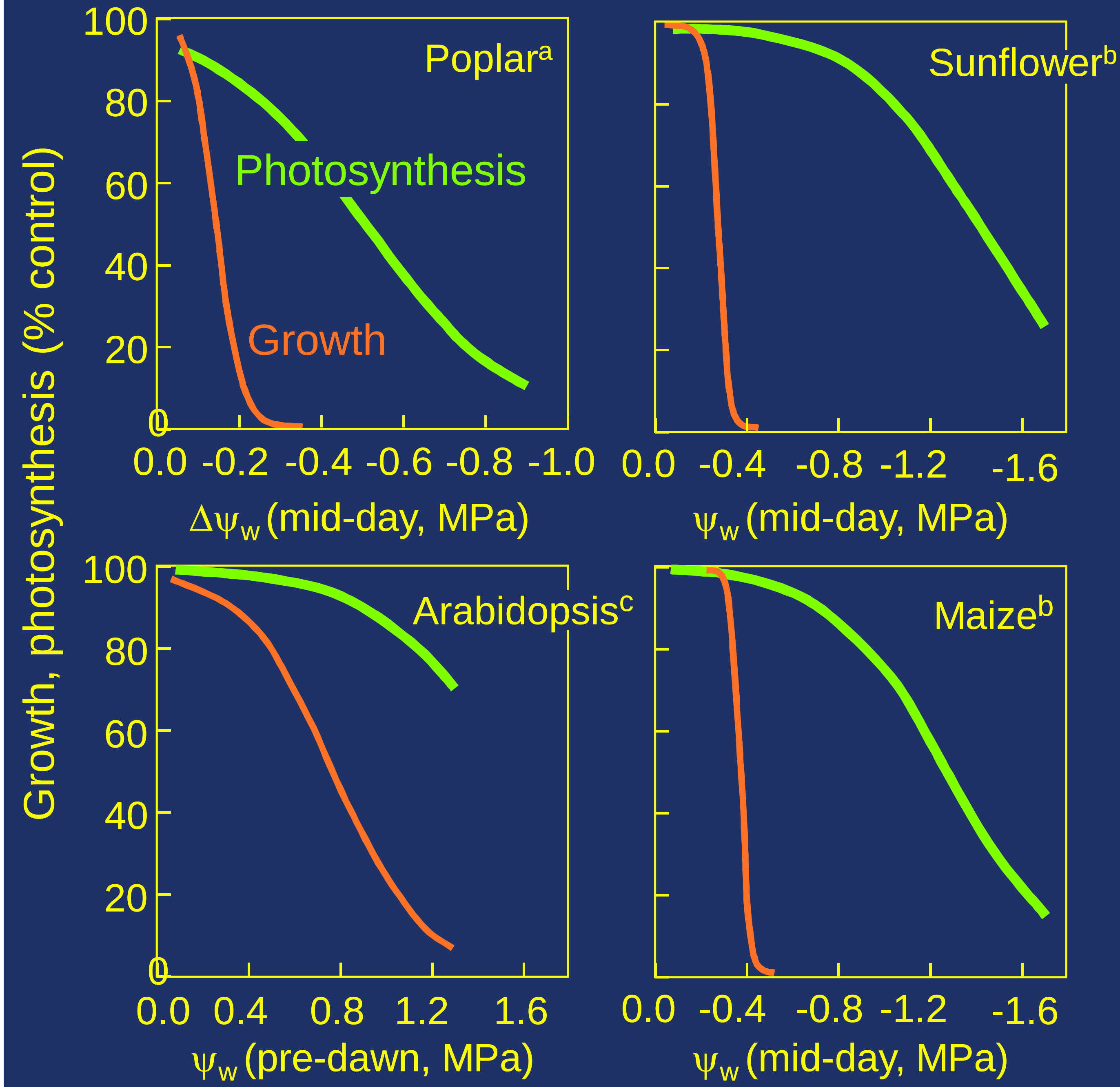
A warmer world may increase R, irrespective of NPP (net loss of C)

A warmer world may increase NPP (C-input) which in turn would stimulate R_s (with no additional T-effect on R_s)

- The only way soil respiration can be de-coupled from NPP in the long run, is a break-down of recalcitrant organic carbon in soils, carbon that is hundreds or thousands of years old.
- Since that break-down - if it does occur - would be very slow, the $R_s = f(NPP)$ relationship would remain largely intact on a year to year basis even in a warmer future.
- on an hour to hour or day to day basis,
  $R = f(T, H_2O)$

Both, drought and low temperature affect sinks first, source activity follows

Differential sensitivity of shoot growth and photosynthesis to soil water deficit.



!

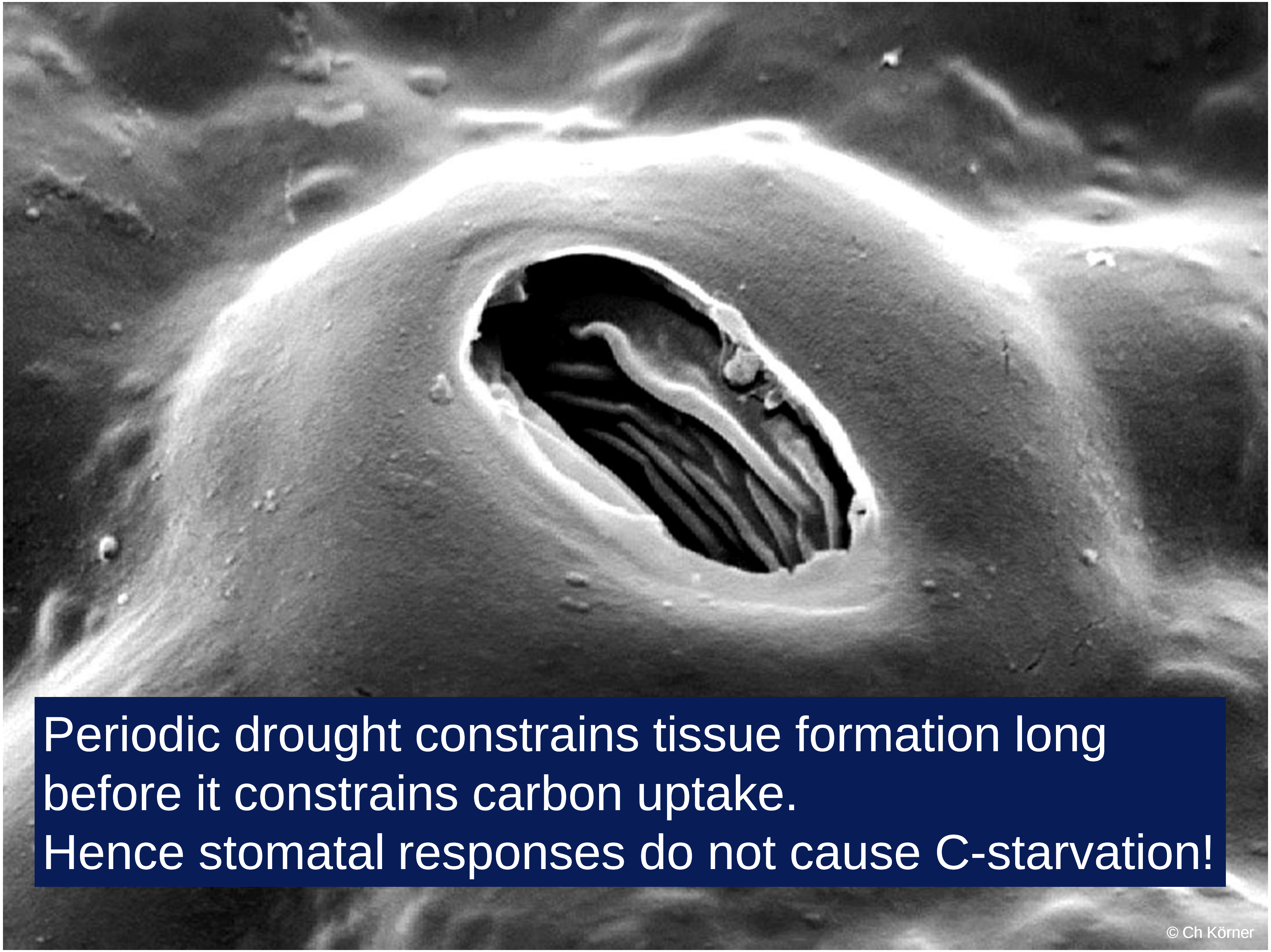
Muller B et al (2011)
J Exp Bot 62:1715

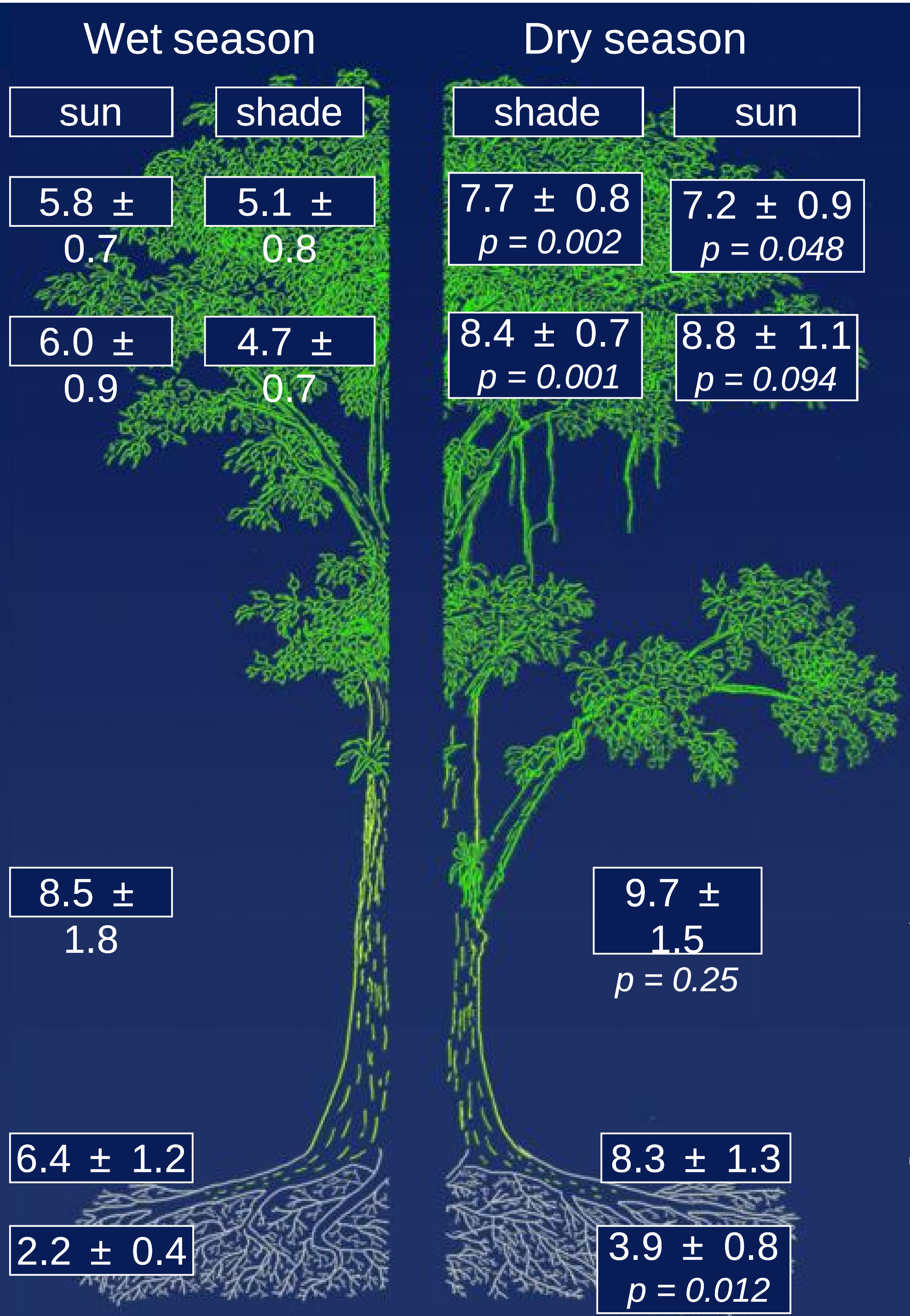
Data from :

[a]Bogeat-Triboullot *et al* (2007)

[b]Boyer (1970), Tardieu *et al* (1999)

[c]Granier *et al* (2006), Hummel *et al* (2010)


Periodic drought constrains tissue formation long before it constrains carbon uptake.
Hence stomatal responses do not cause C-starvation!
© Ch Körner



Seasonal variation of NSC in tropical tree species

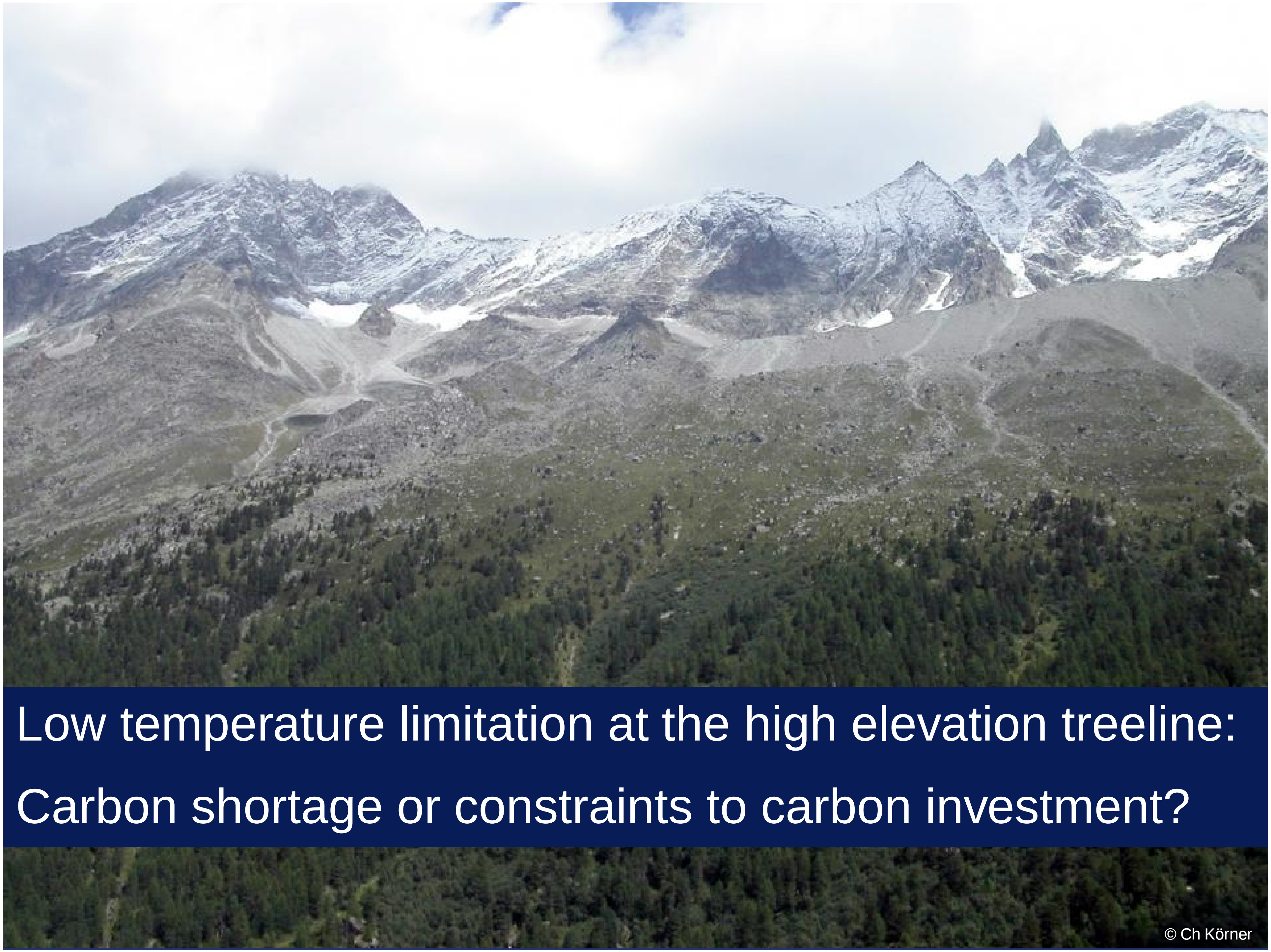
Sink limitation:

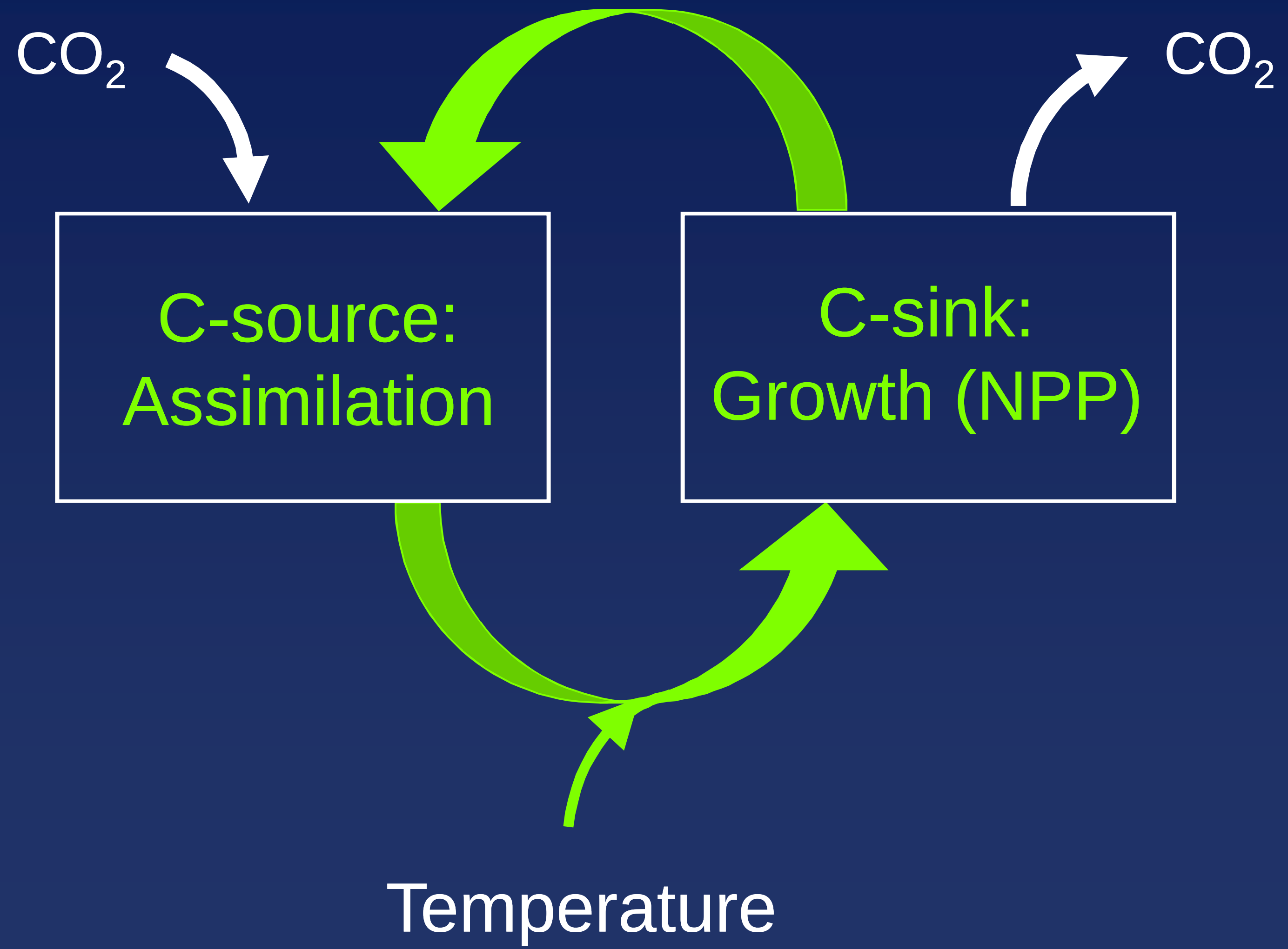
Drought affects tissue formation first, photosynthesis last.

→ NSC ↑

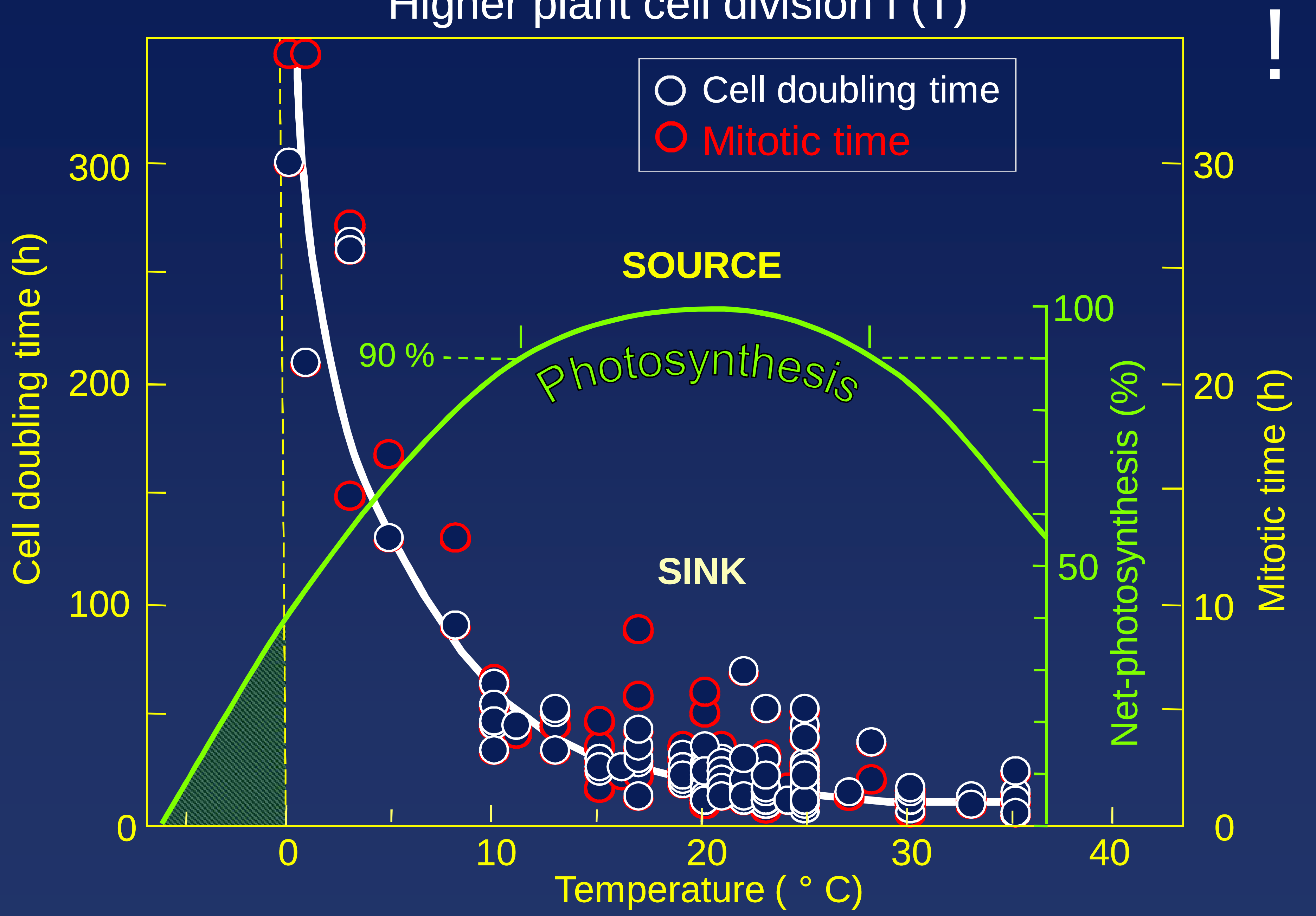
M Würth *et al* (2005) Oecologia 143:11

Low temperature limitation at the high elevation treeline: Carbon shortage or constraints to carbon investment?

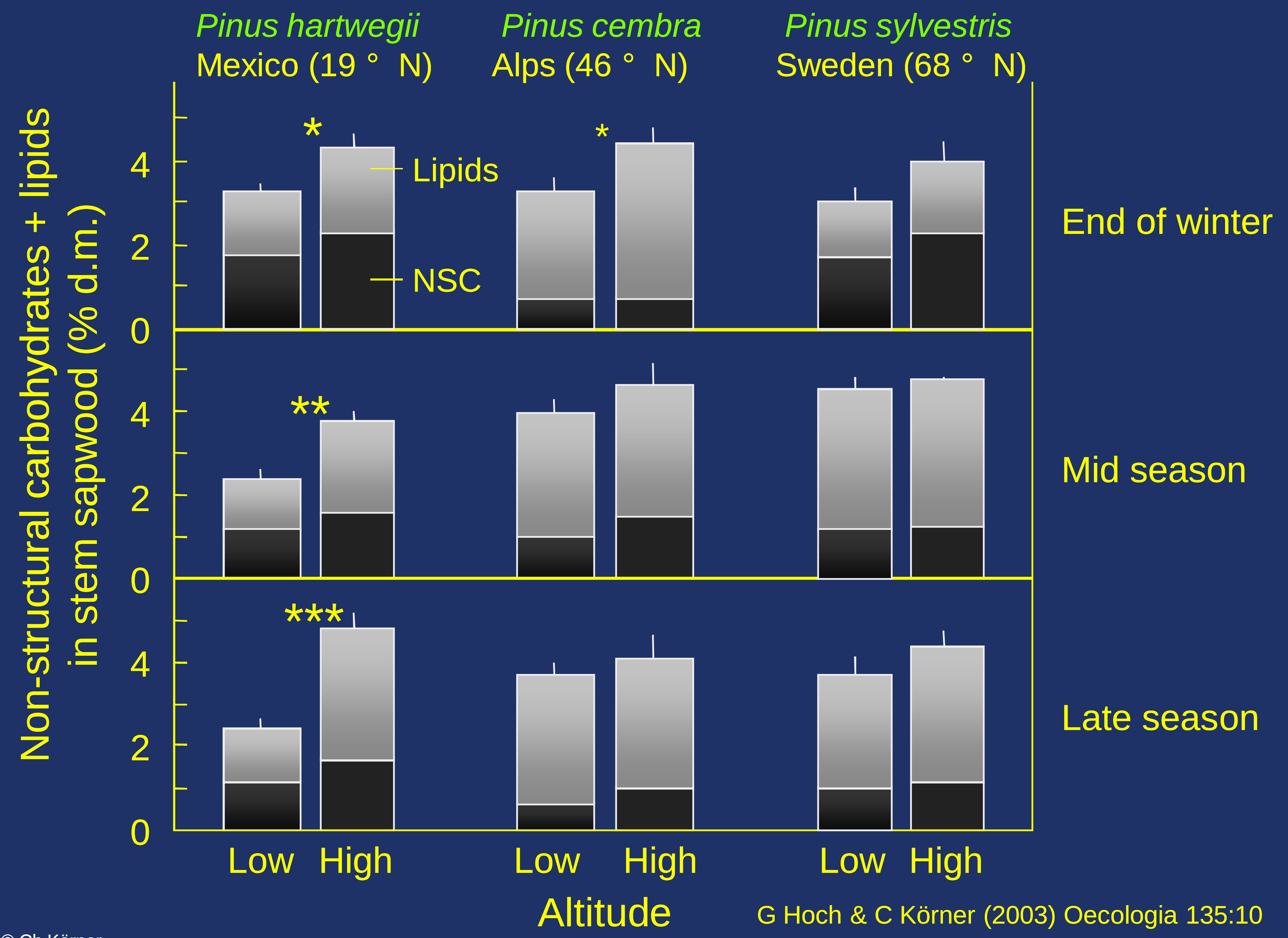



CO2
CO2
C-source:
Assimilation
C-sink:
Growth (NPP)
Temperature

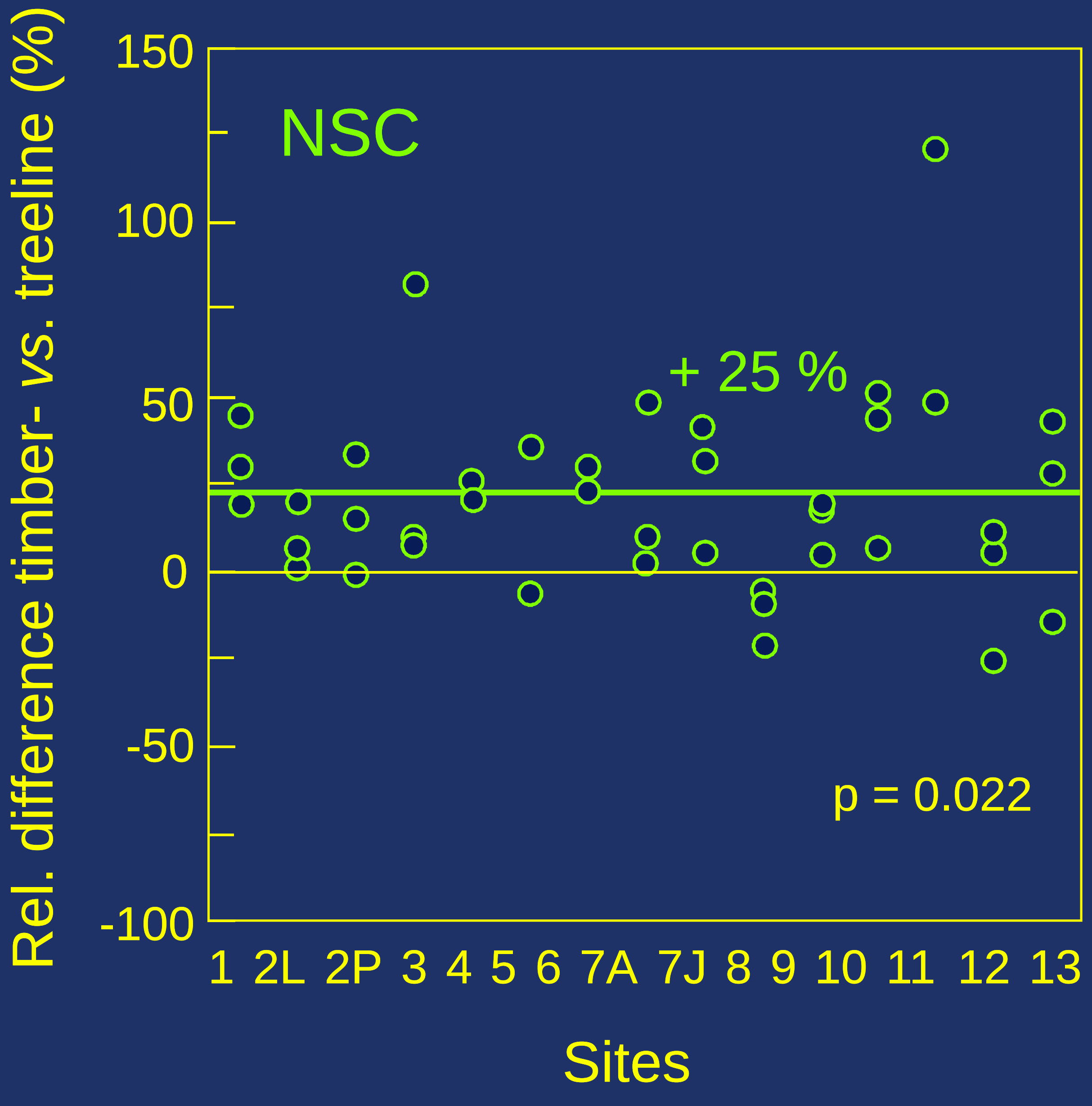
Higher plant cell division f (T)



Ch Körner (2003) *Alpine Plant Life*. Springer, Berlin



G Hoch & C Körner (2003) Oecologia 135:10



G Hoch & Ch Körner, unpubl.

Classics in agroscience:

The ‘magic‘ 6 ° C threshold

- "There seems to be a 6 ° C threshold temperature for plant development" (De Candolle, 1855).
- "The advent of spring may properly be considered as taking place at the advent of a 6-7 ° C isotherm" (Harrington, 1894).
- "6 ° C is considered the zero point of vital temperature" (USDA, Smith, 1920).

Plant growth in elevated CO_2

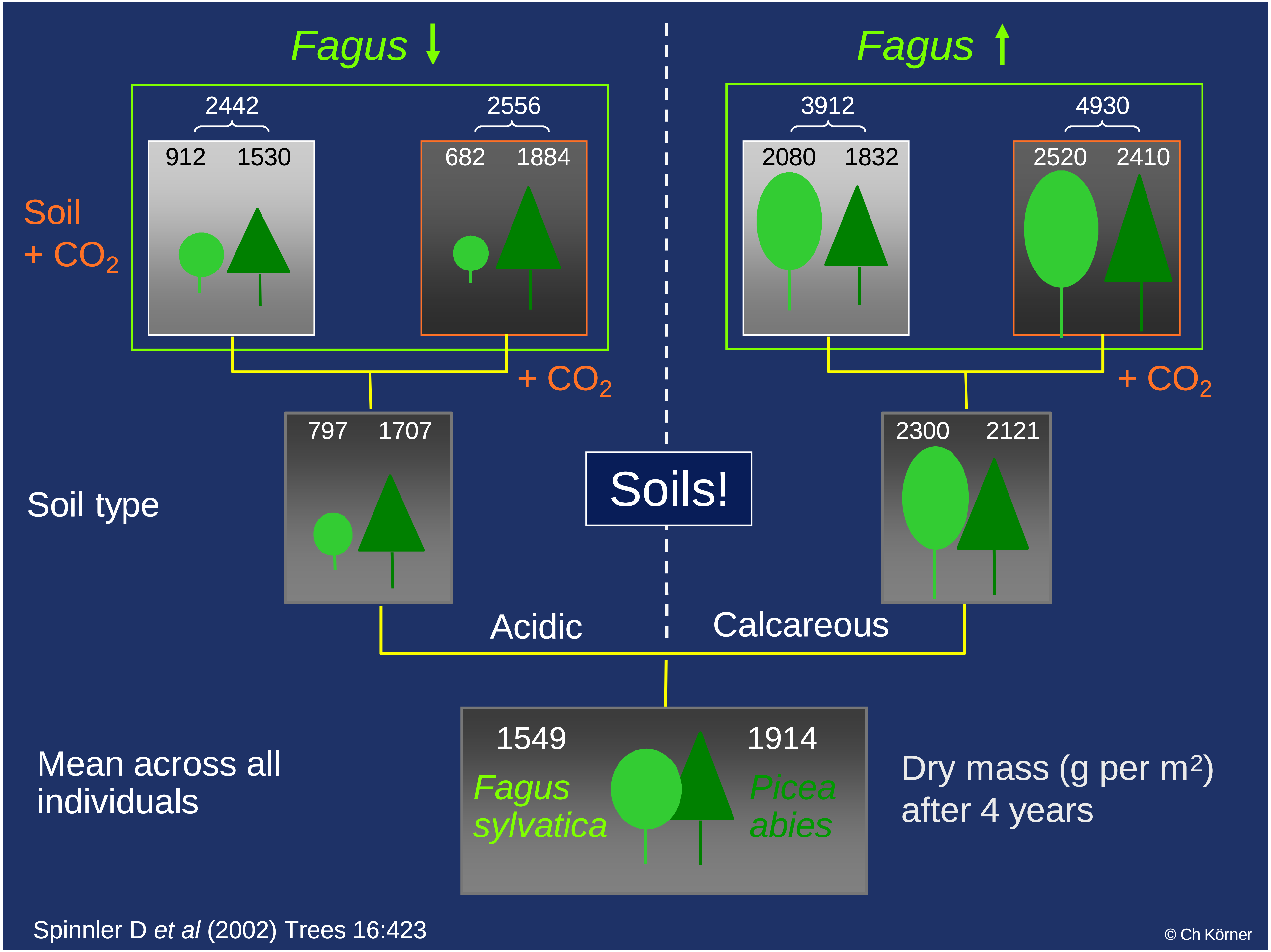
- Decoupled systems (horticulture)
- Expanding systems (in transition) → Coupled systems (‘steady state‘)

Coupling:
- steady state fine root turnover
- steady state N-cycle
- steady state litter production (LAI)

Ch Körner (2006) Tansley Review, New Phytol 172:393

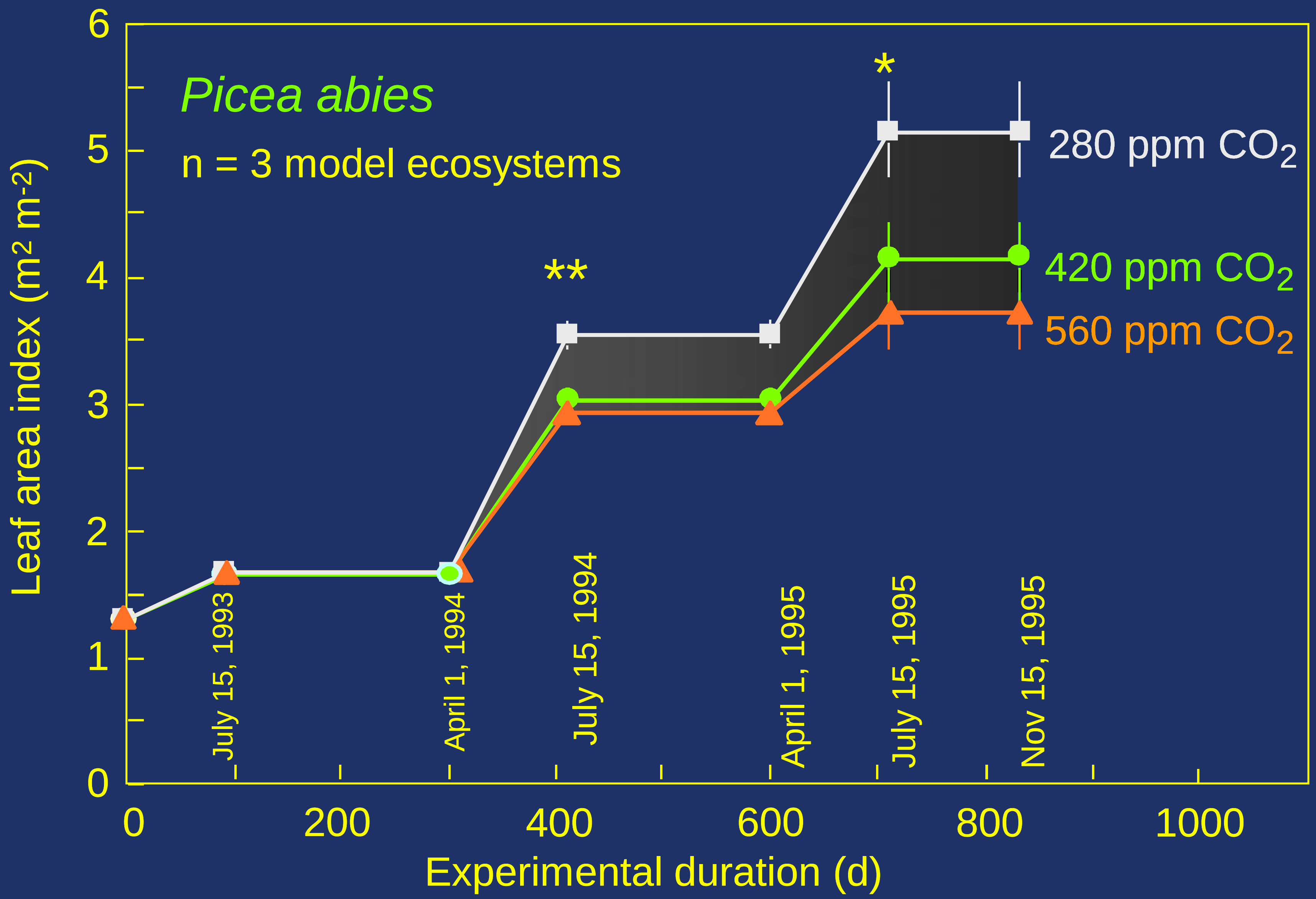

Decoupled horticultural system
© Ch Körner


Expanding system
© Ch Körner



Fagus ↓
2442
912 1530
2556
682 1884
Fagus ↑
3912
2080 1832
4930
2520 2410
Soil
+ CO_2
+ CO_2
+ CO_2
797 1707
2300 2121
Soils!
Soil type
Acidic
Calcareous
Mean across all individuals
1549
1914
Fagus sylvatica
Picea abies
Dry mass (g per m²) after 4 years
Spinnler D *et al* (2002) Trees 16:423
© Ch Körner

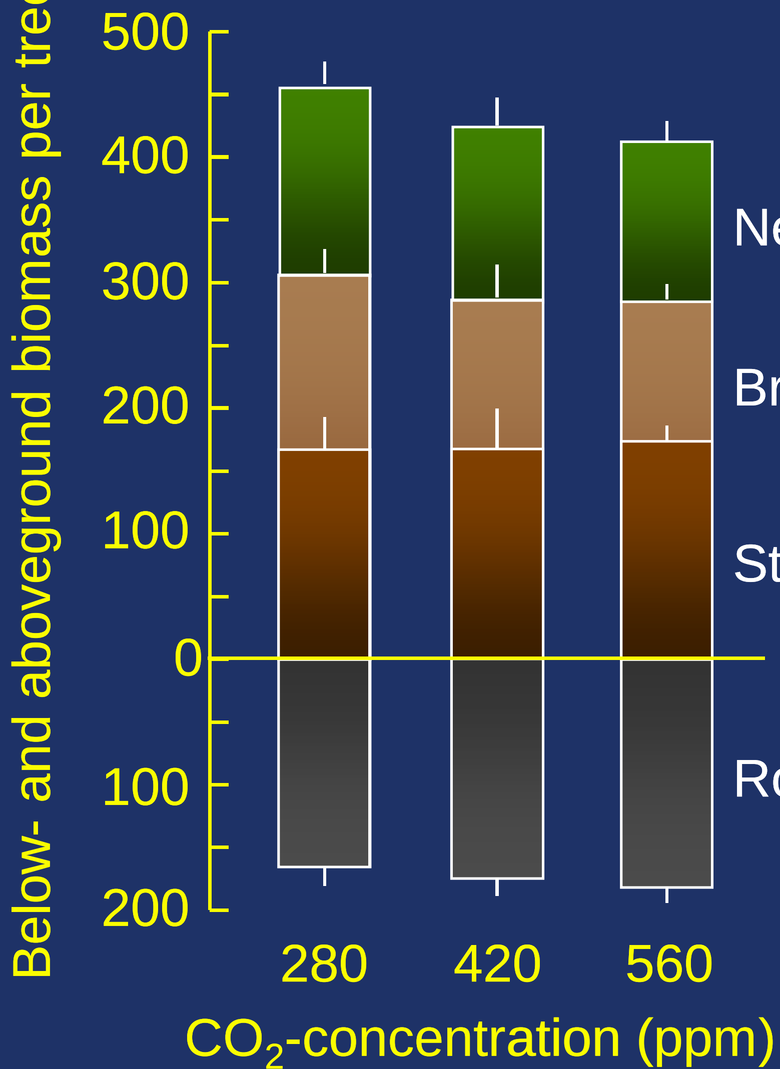
CO_2-induced nutrient shortage: LAI ↓



S Hättenschwiler & Ch Körner (1998) Oecologia 113:104

Picea abies biomass

n = 3 model ecosystems



S Hättenschwiler & C Körner (1998) Oecologia 113:104

Contradictory responses to elevated CO_2 after >10 years

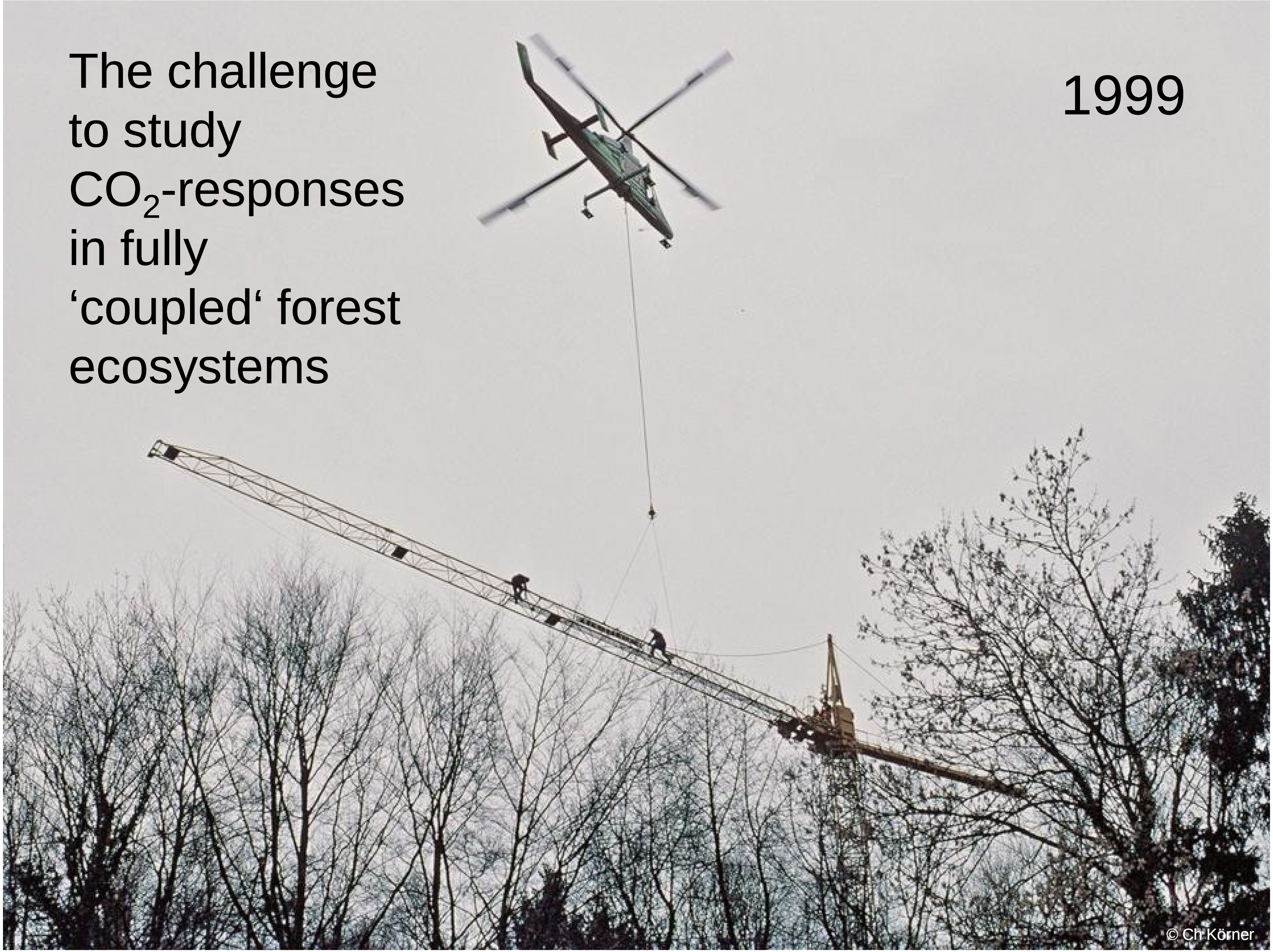
Duke FACE:
stem radial growth enhanced

Oak Ridge FACE:
no effect
(roots responding in the early phase)

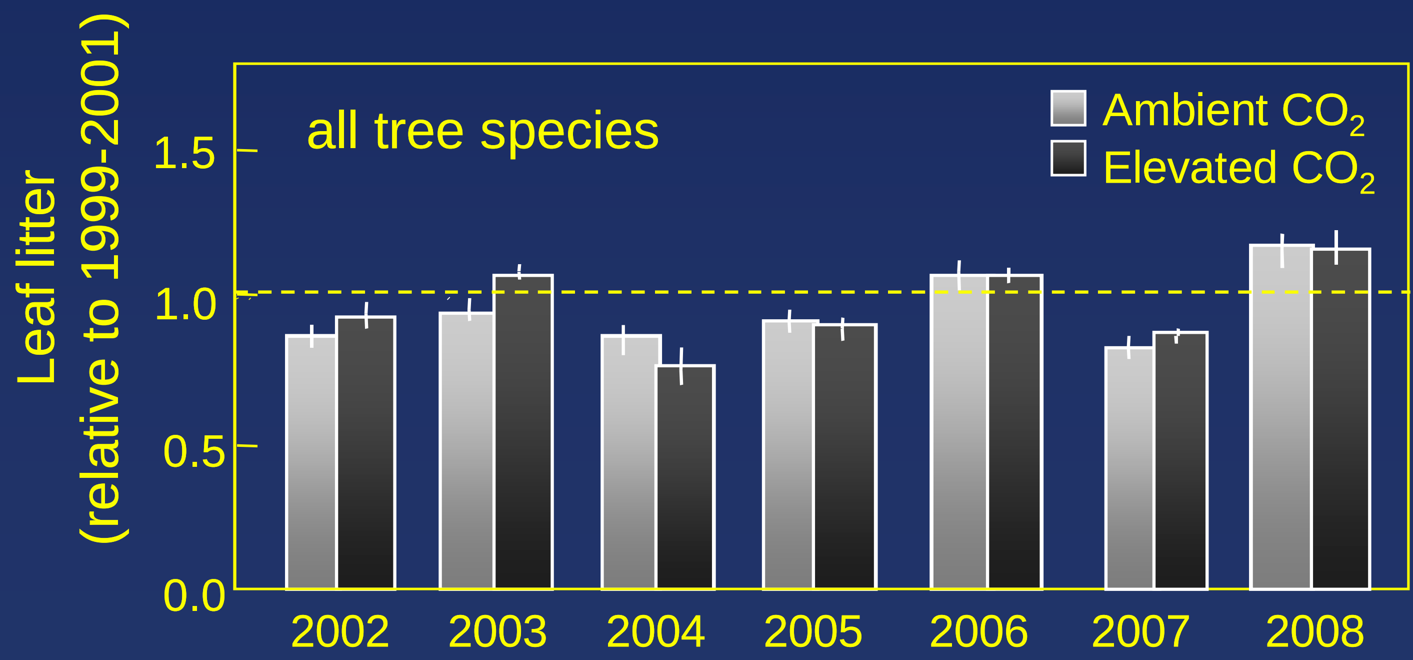
Species or site effect?

The challenge to study CO_2-responses in fully ‘coupled‘ forest ecosystems

1999



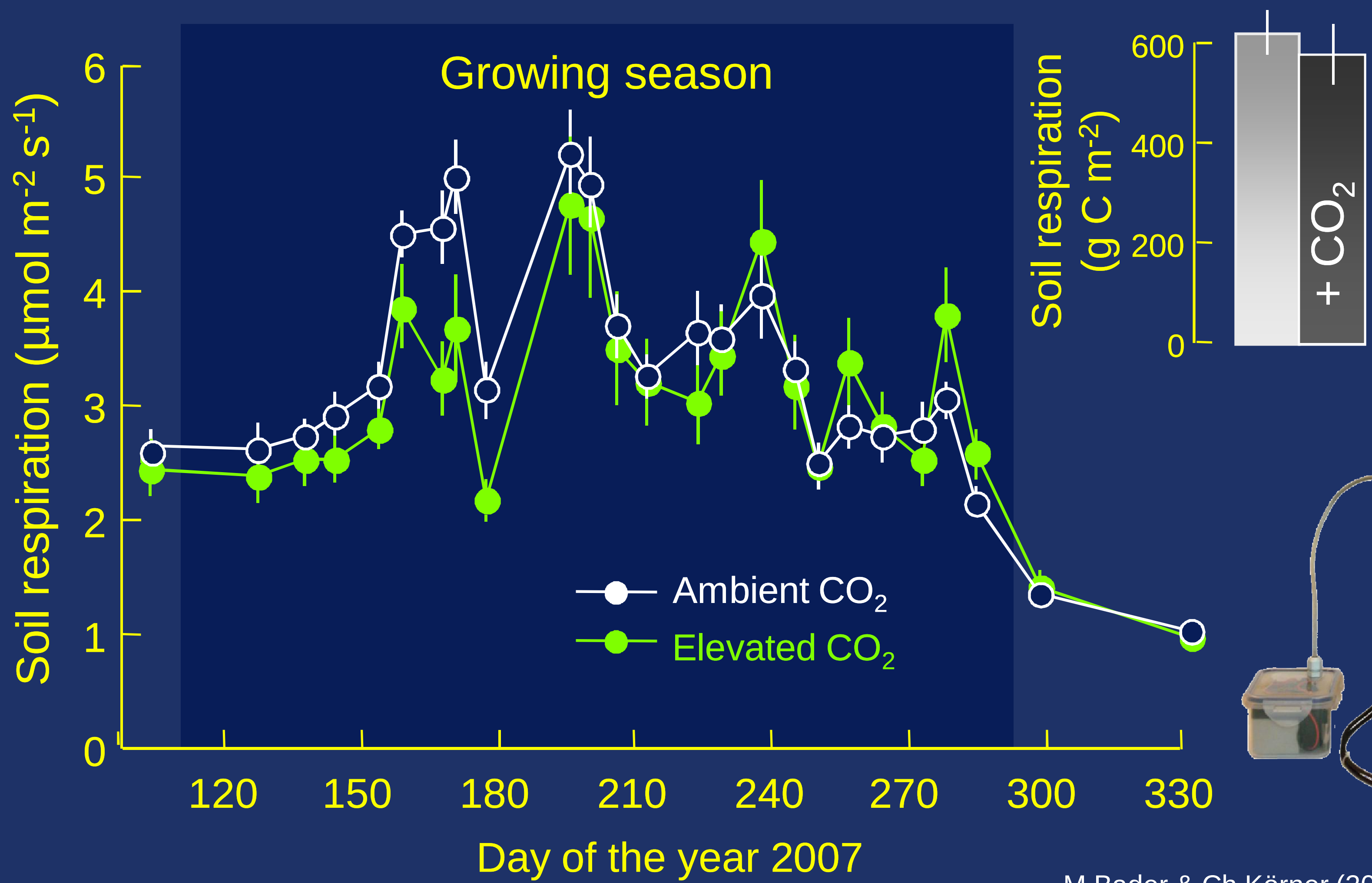
Leaf litter



No response

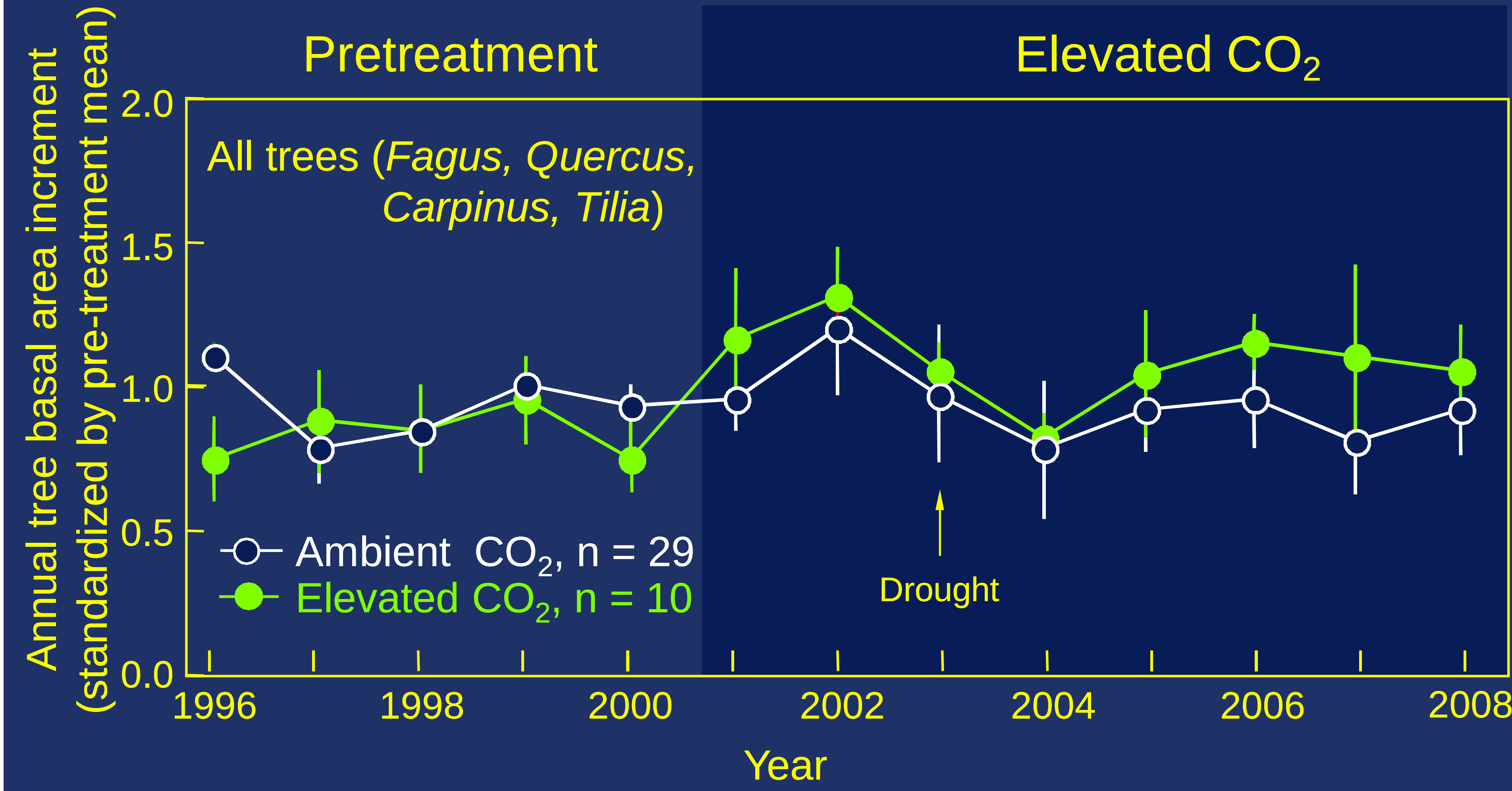
Ch Körner *et al.* (2005) Science 309:1360 and new data

CO_2 - release from soil - no response after 7 years



M Bader & Ch Körner (2010)
Glob Change Biol 16:2830

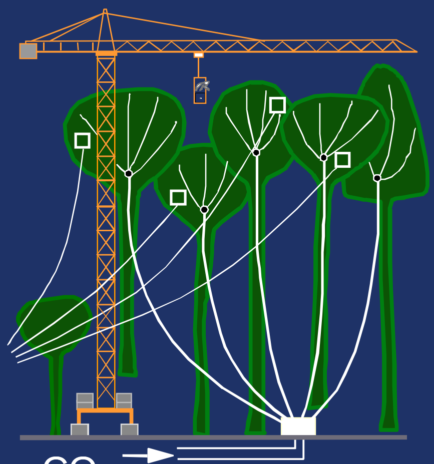
Growth of 100 year old trees in elevated CO_2, Swiss web-FACE



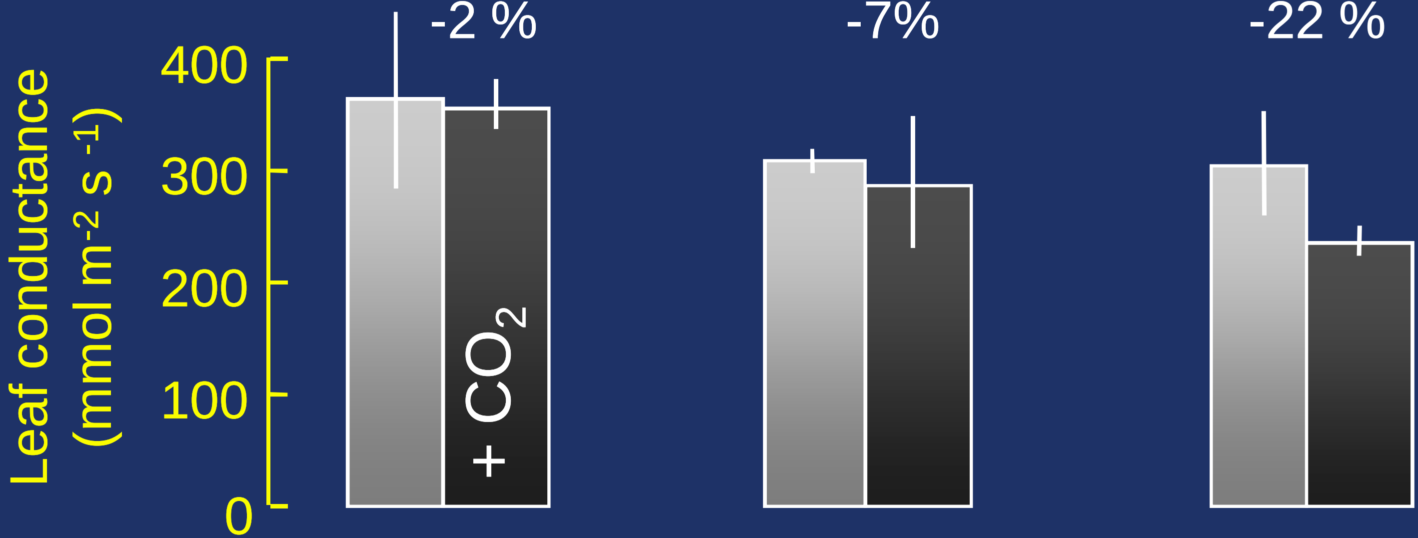
Ch Körner *et al.* (2005) Science 309:1360 and new data

Stomatal response to elevated CO_2

Swiss web-FACE



• None	• Weak	• Strong
		
Quercus	*Fagus*	*Carpinus*



S Keel *et al* (2007) Trees 21:151

Species differ in their responses

↓

Biodiversity effects

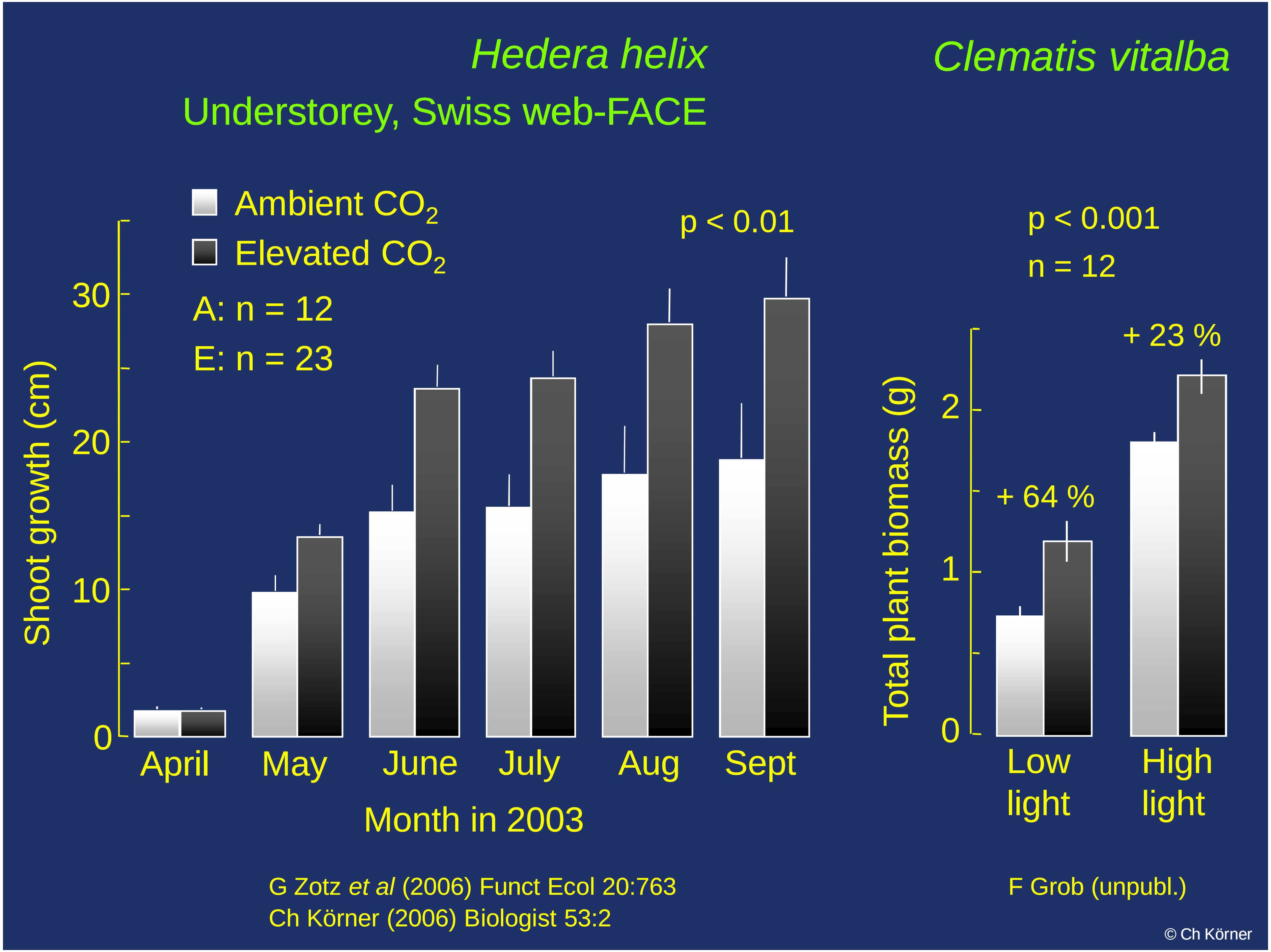
(winners and losers, new assemblages)

↓

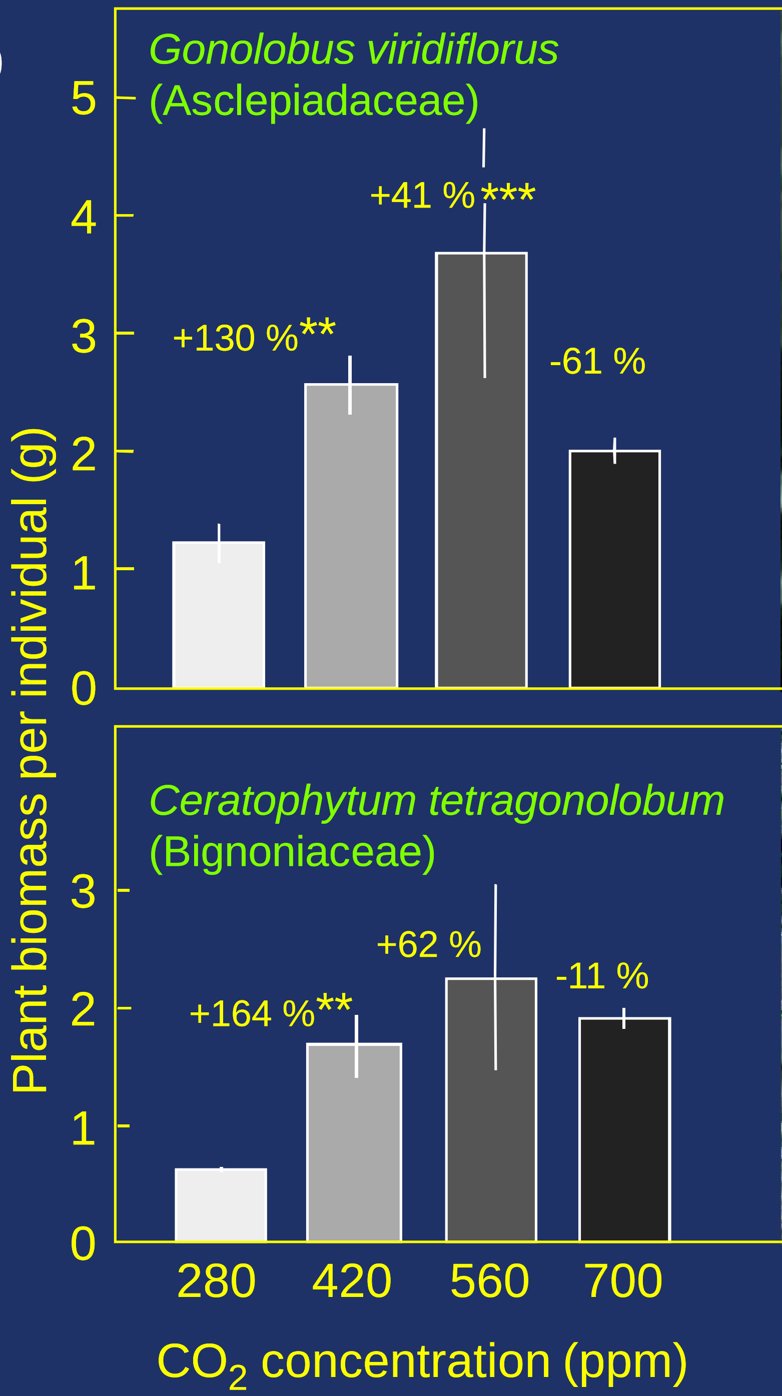
Ecosystem effects

(water loss, carbon and nutrient cycle)

→ 2 examples


Hedera helix
Understorey, Swiss web-FACE
Ambient CO_2
Elevated CO_2
A: n = 12
E: n = 23
p < 0.01
Shoot growth (cm)
0
10
20
30
April
May
June
July
Aug
Sept
Month in 2003
Clematis vitalba
p < 0.001
n = 12
+ 23 %
+ 64 %
Total plant biomass (g)
0
1
2
Low light
High light
G Zotz et al (2006) Funct Ecol 20:763
Ch Körner (2006) Biologist 53:2
F Grob (unpubl.)
© Ch Körner

In deep shade, lianas are gaining



J Granados & Ch Körner (2002) GCB 8:1109
Ch Körner (2003) Phil Trans R Soc Lond A 361:2023

Summary CO_2 effects

- First principle responses (e.g. photosynthetic or stomatal CO_2-responses) might become overrun by biodiversity effects in the long term.
- Elevated atmospheric CO_2 is unlikely to cause a sustained increase of carbon storage in biomass even if it stimulates growth.
- All experimental data are confounded by stomata mediated water effects.
- Deep shade is the most likely pace to see positive CO_2-signals.

Ch Körner (2009) Annu Rev Evol Syst 40:61-79

Overall summary

- Carbon capture is controlled by C-sinks.
- C-sinks are controlled by soil resources (nutrients, water, stoichiometry constraints).
- Ecosystem respiration is controlled by substrate availability (NPP) rather than T.
- Drought and low temperature act upon sink activity.
- Ecosystem CO_2-saturation because sink activity controls source activity and because soil resources are finite.
- Life in deep shade is intrinsically C-limited.
- Biodiversity and its change affects the C-cycle.