

The biology of the carbon cycle: a paradigm shift

- Carbon source-sink relations
- Carbon fluxes and carbon pools
- Elevated CO₂
- Species range limits and phenology

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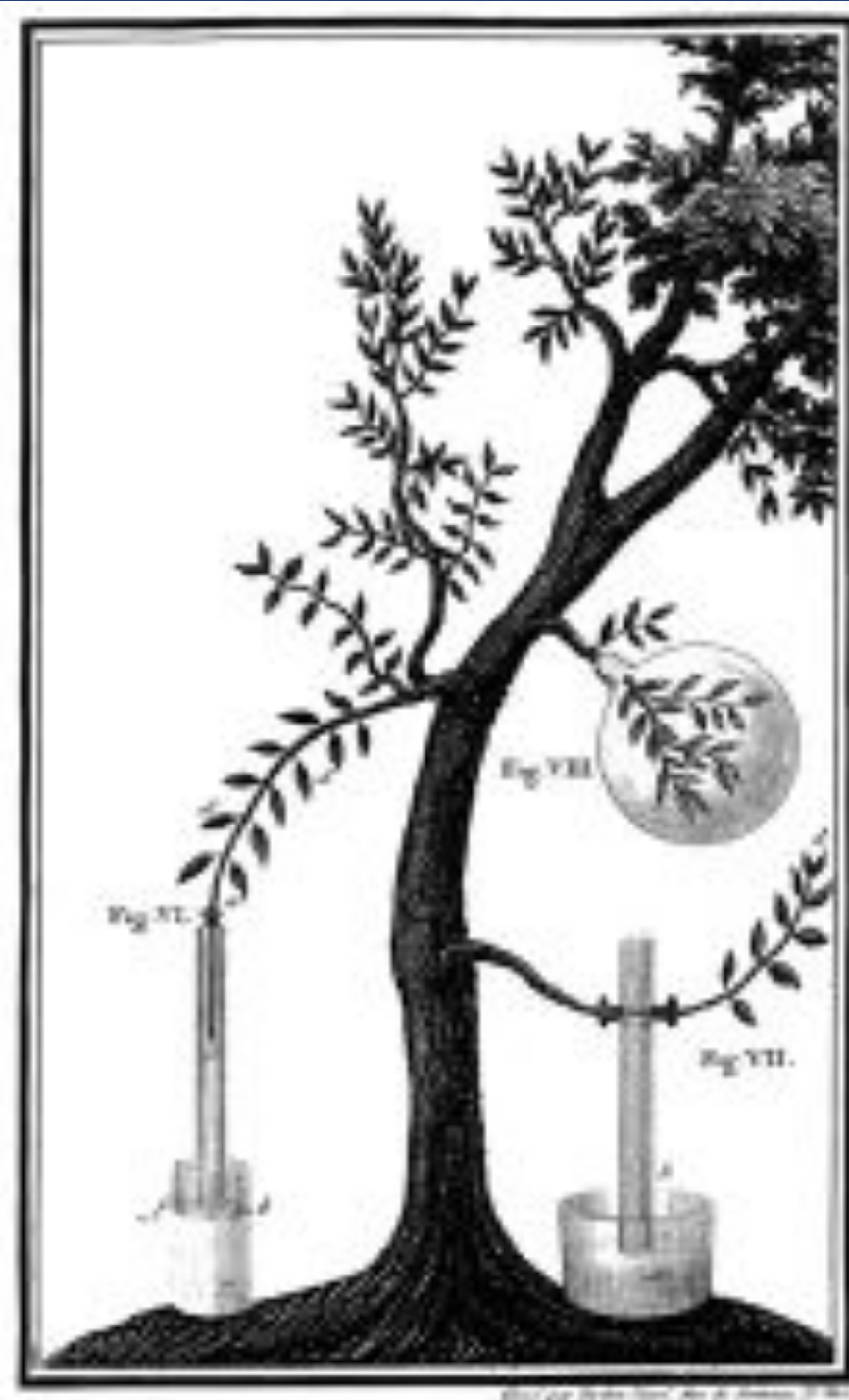
In Geneva 210 years ago:

'The primary plant food comes from air'

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

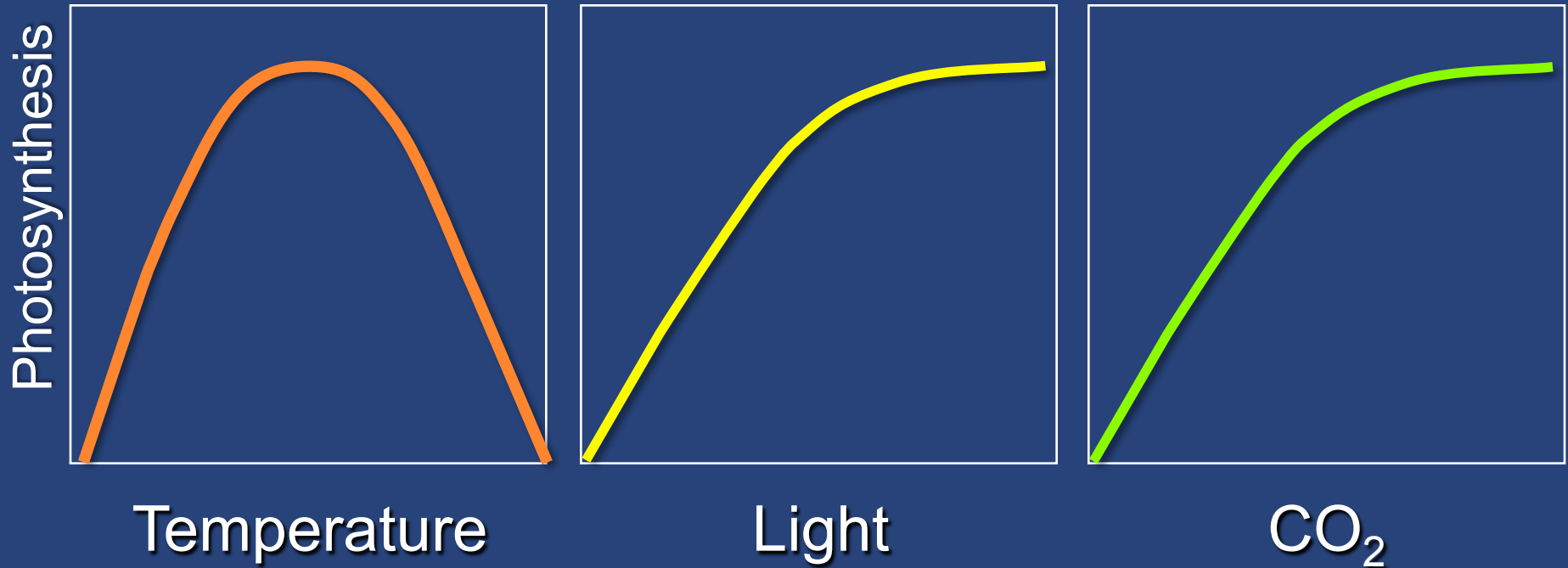
Paving the road:

- **Jan Ingenhousz (1779)**
Experiments upon vegetables, discovering their great power of purifying the common air in the sun-shine, and of injuring it in the shade and at night. P. Elmsly and H. Payne, London, UK.
- **Jean Senebier (1783)**
Recherches sur l'influence de la lumière solaire pour métamorphoser l'air fixe en air pur par la végétation. Barthelemi Chirol, Geneva, Switzerland.



The carbon centric view starts here ...

$$A = f(T, \text{PFD}, \text{CO}_2)$$



Sources rarely control sinks



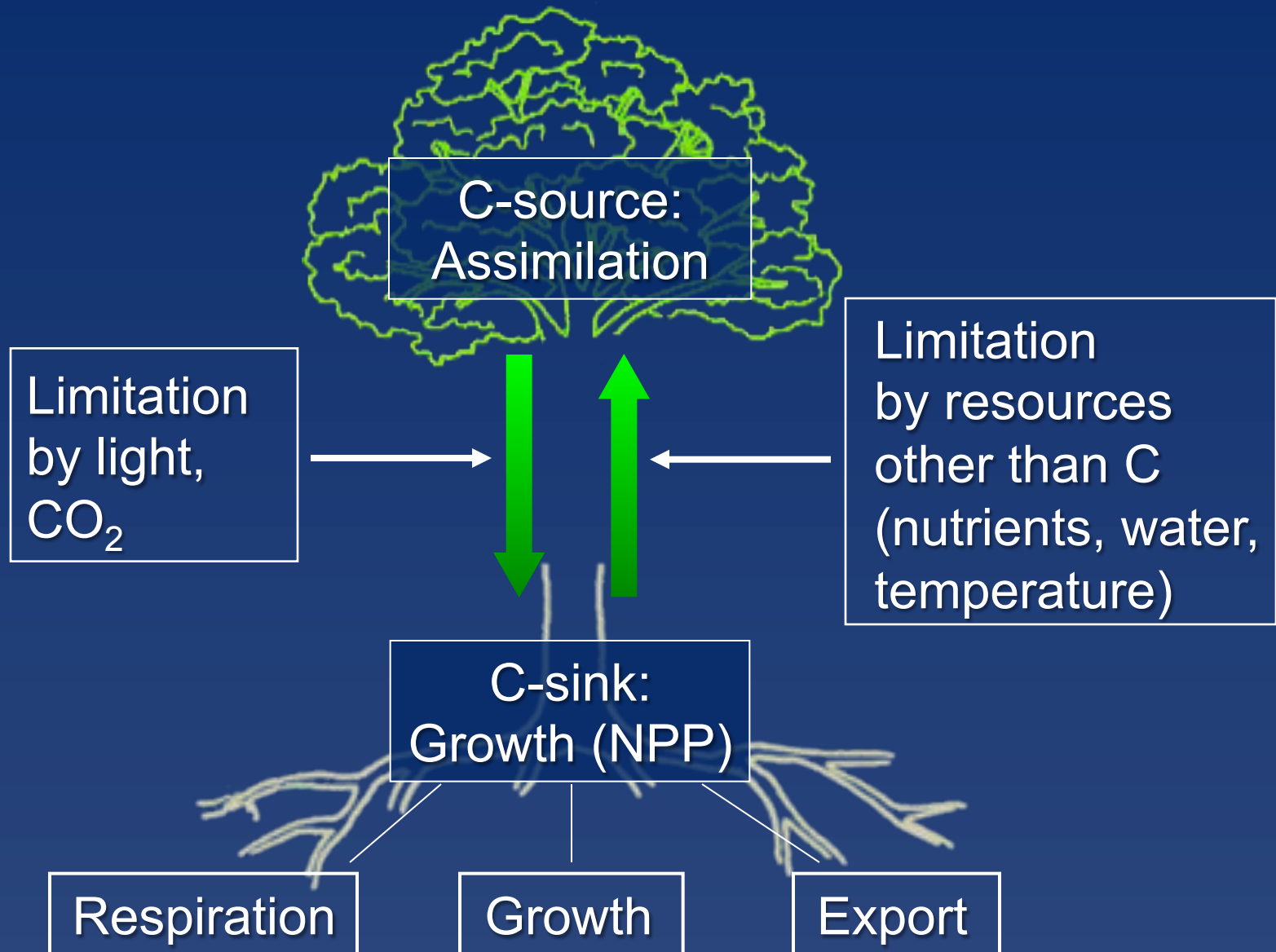
Source
(photosynthesis)

Transport of
building material

Sink
(growth)



Carbon uptake and carbon use by plants



For instance, drought and low temperature affect sinks first, source activity follows



Drought: sinks affected first

Water shortage:

Old

Stomatal closure
and inhibition of
photosynthesis

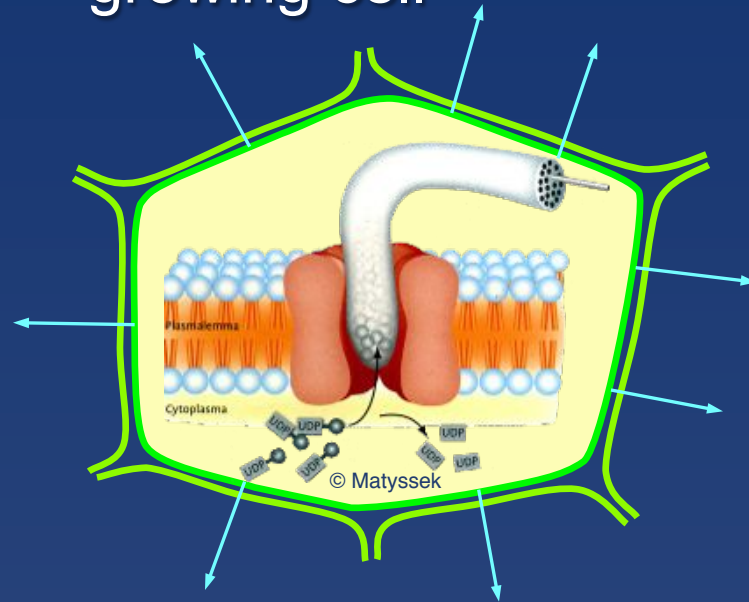


-1.2 to -2.0 MPa

Source

New

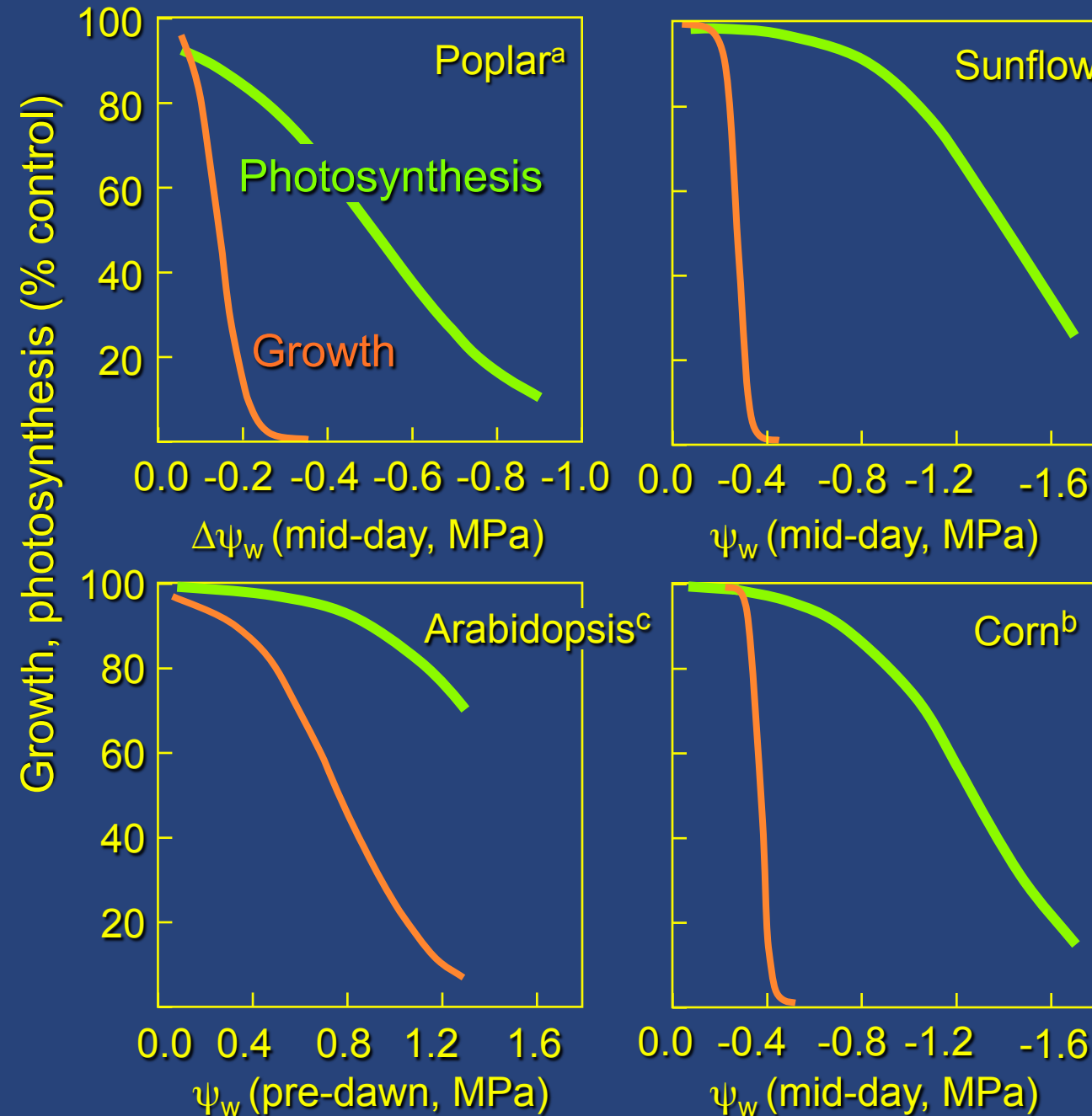
Turgor driven yielding
of the cell wall in a
growing cell



-0.5 to -1.0 MPa

Sink

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



!

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

Data from :

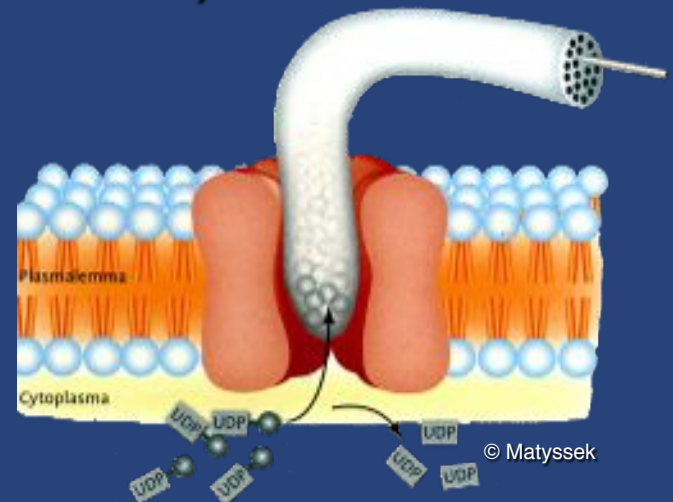
^aBogeat-Triboulot *et al* (2007)

^bBoyer (1970),
Tardieu *et al* (1999)

^cGranier *et al* (2006),
Hummel *et al* (2010)

Water shortage acts on sinks first

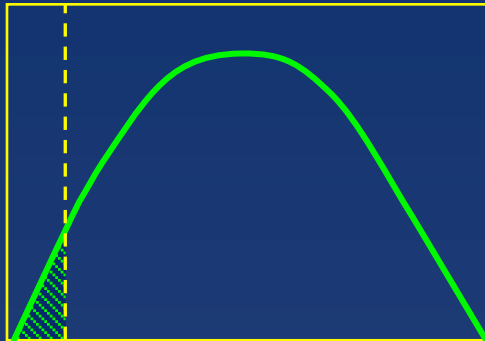
- Turgor controls tissue formation.
- Carbohydrate transport is not constrained, hence distant stores are filled.
- Carbohydrate downloading and storage are ensuring an operative photosynthetic machinery (no endproduct inhibition).



Low temperature: sinks stop first

Old

Photosynthesis



zero at -6 °C

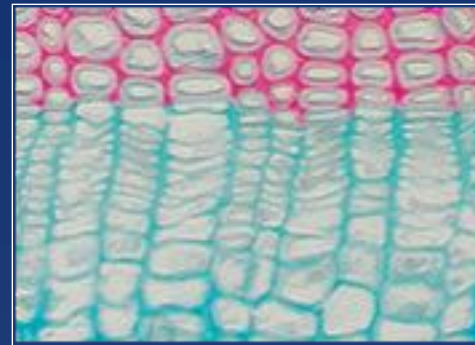
30-40 % at 0 °C

50-70 % at +5 °C

Source

New

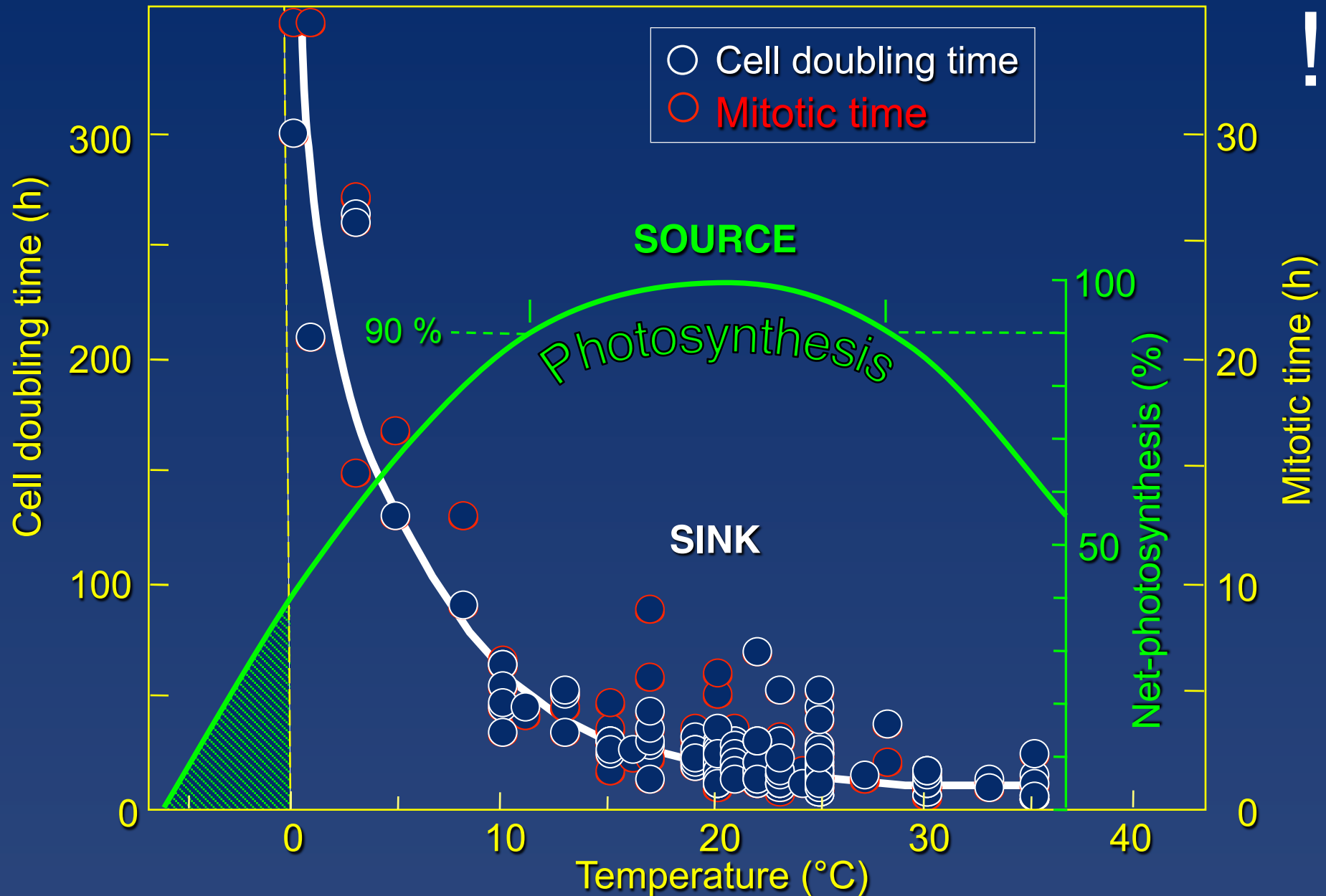
Cambium



No cell differentiation < +5 °C
(Cell division is robust)

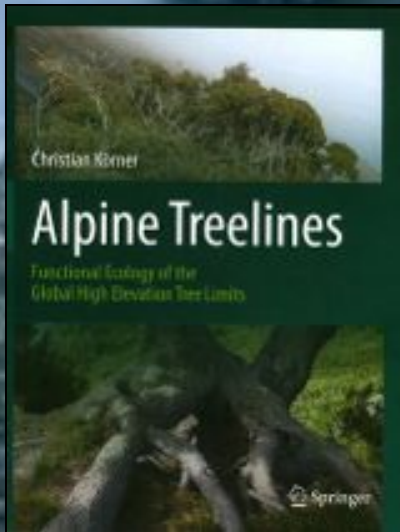
Sink

Different processes have different T sensitivity



Treeelines will move sooner or later ...

The cold edge



Xylogenesis and
root extension
growth approach
zero at +5 °C

- Rossi S *et al* (2007)
Oecologia 152:1
- Alvarez-Uria P & Körner C
(2007) Funct Ecol 21:211

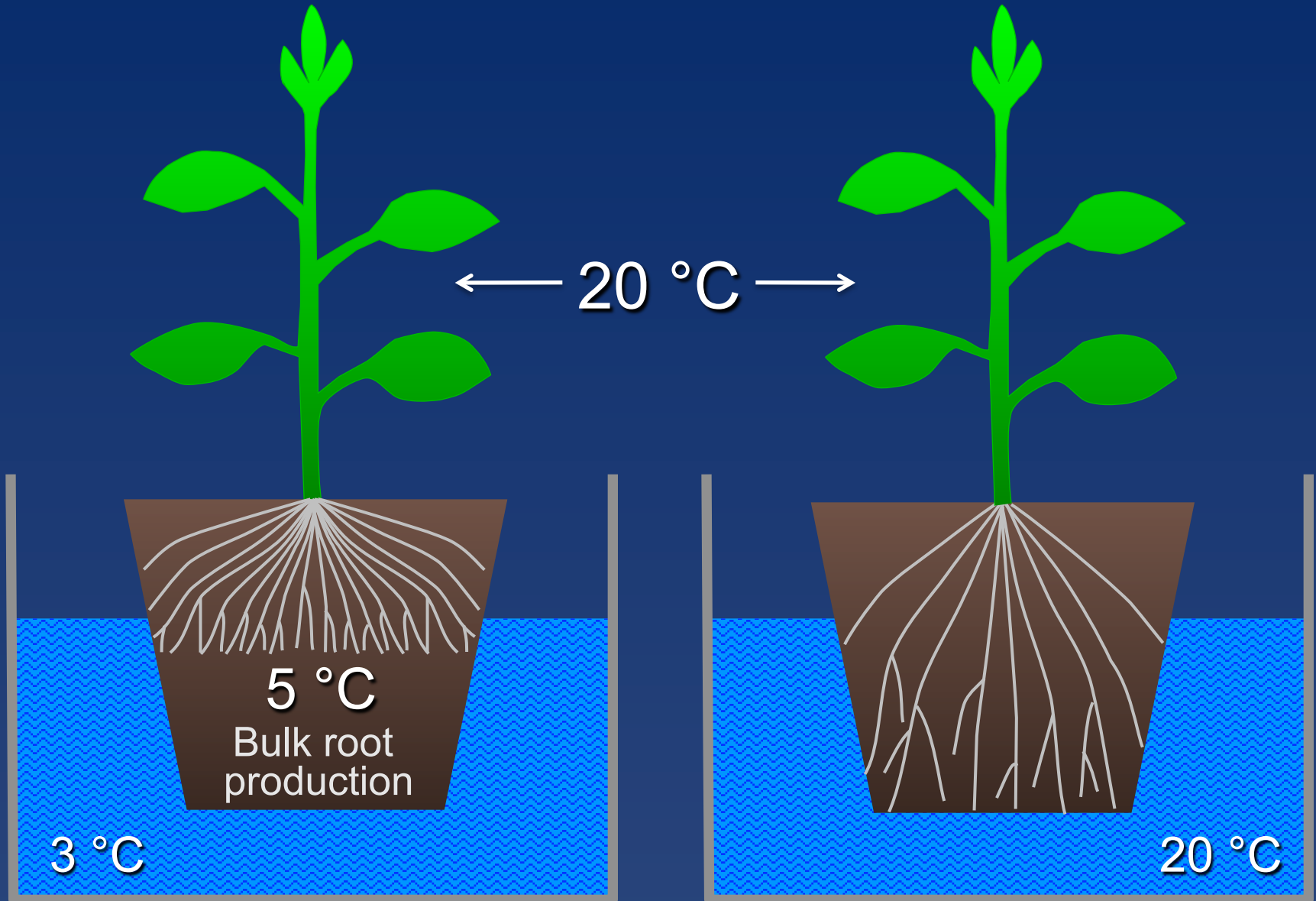
Xylem

Cambial zone

Phloem



C-limitation or shutdown of tissue formation at low temperature?



Nutrient limitation: stoichiometry of C sinks controls C incorporation

→ Healthy life needs 25 essential chemical elements

Old

More photosynthates permit capturing elements other than C



New

Nutrients control the amount of C that can be taken up

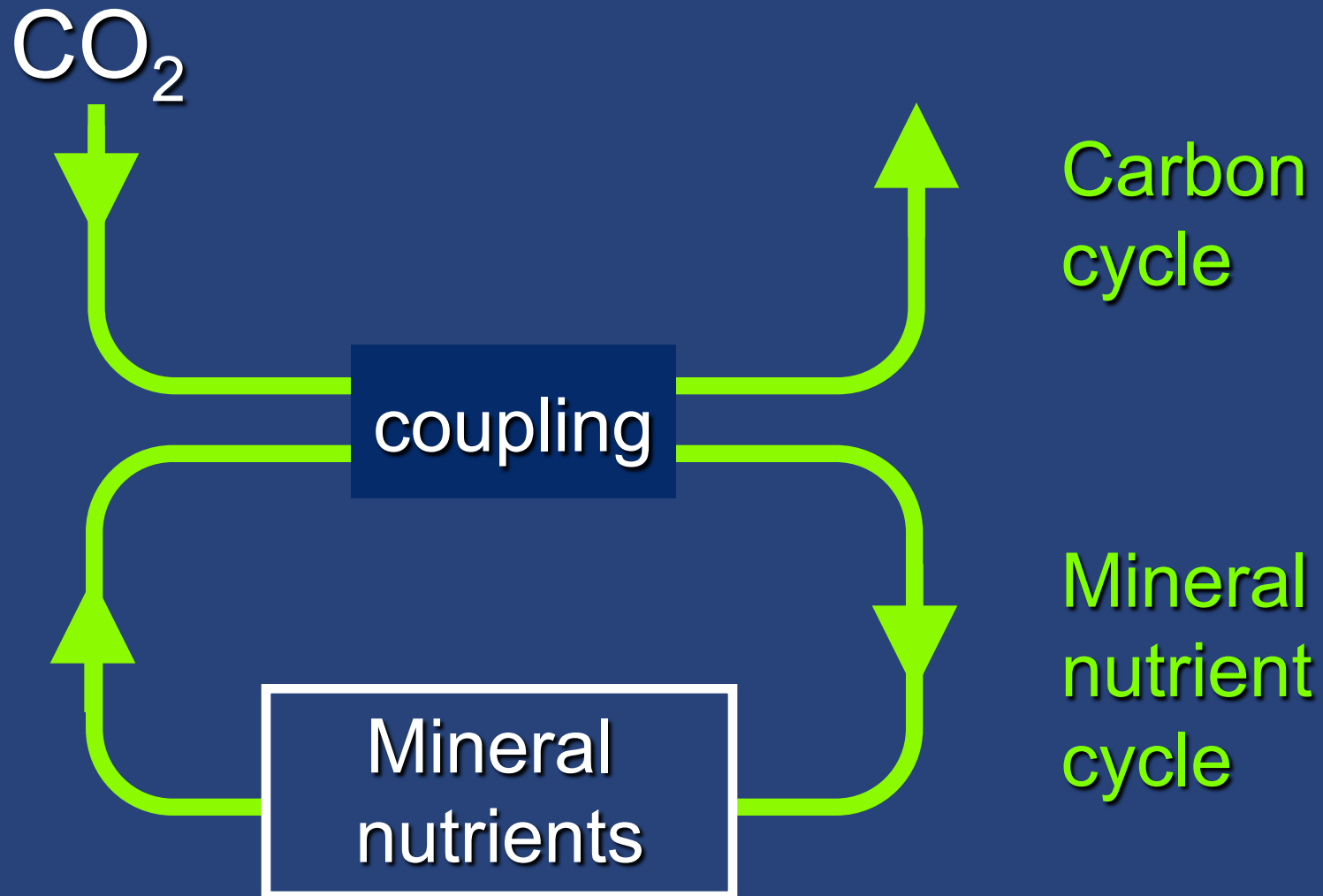


A periodic table of elements is shown. A green bracket highlights the group of elements from Carbon (C) to Fluorine (F) in the second period. A red arrow points to the Nitrogen (N) element.

... a few are redundant, but >25 are essential (not just N!)

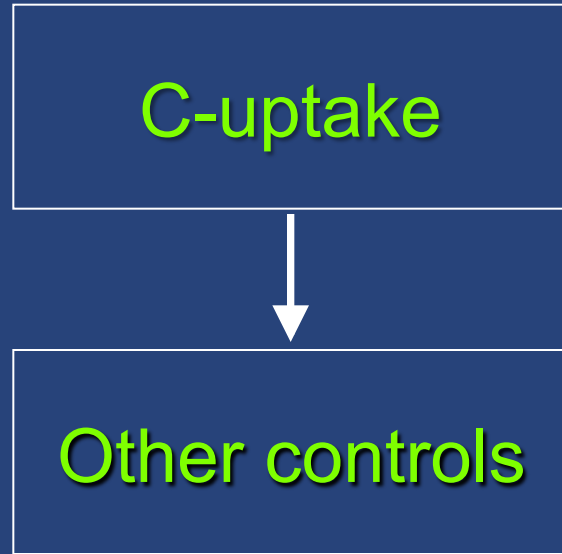
In: Sterner RW & Elser JJ (2002) Ecological Stoichiometry. Princeton Univ Press, Princeton

The mineral cycle controls the carbon cycle



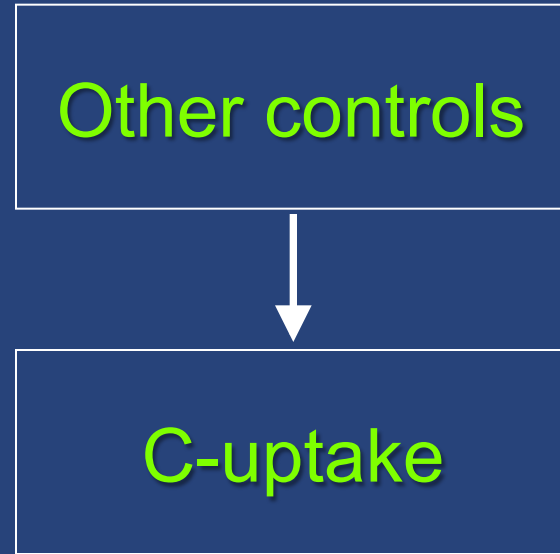
Priority in theory and modeling of plant growth or NPP

Old model
(carbon centric)



Per unit leaf area
CO₂ acquisition has
priority over any
other growth control

New model
(sinks control sources)



Meristem activity
determines
C-demand

Summary on source-sink relationships

- Carbon uptake is largely controlled by C-sinks.
- Drought and low temperature act upon sink activity first (meristems).
- CO₂-saturation because **sinks control source activity** and because soil resources (nutrients) are finite.

Source driven growth models yield plausible results for the wrong reason.

Fatichi S *et al* (2014) New Phytol 201:1086

Growth, NPP

NPP = Net primary production
sensu annual biomass C production

NEP = Net ecosystem production
sensu C storage

C

NEP

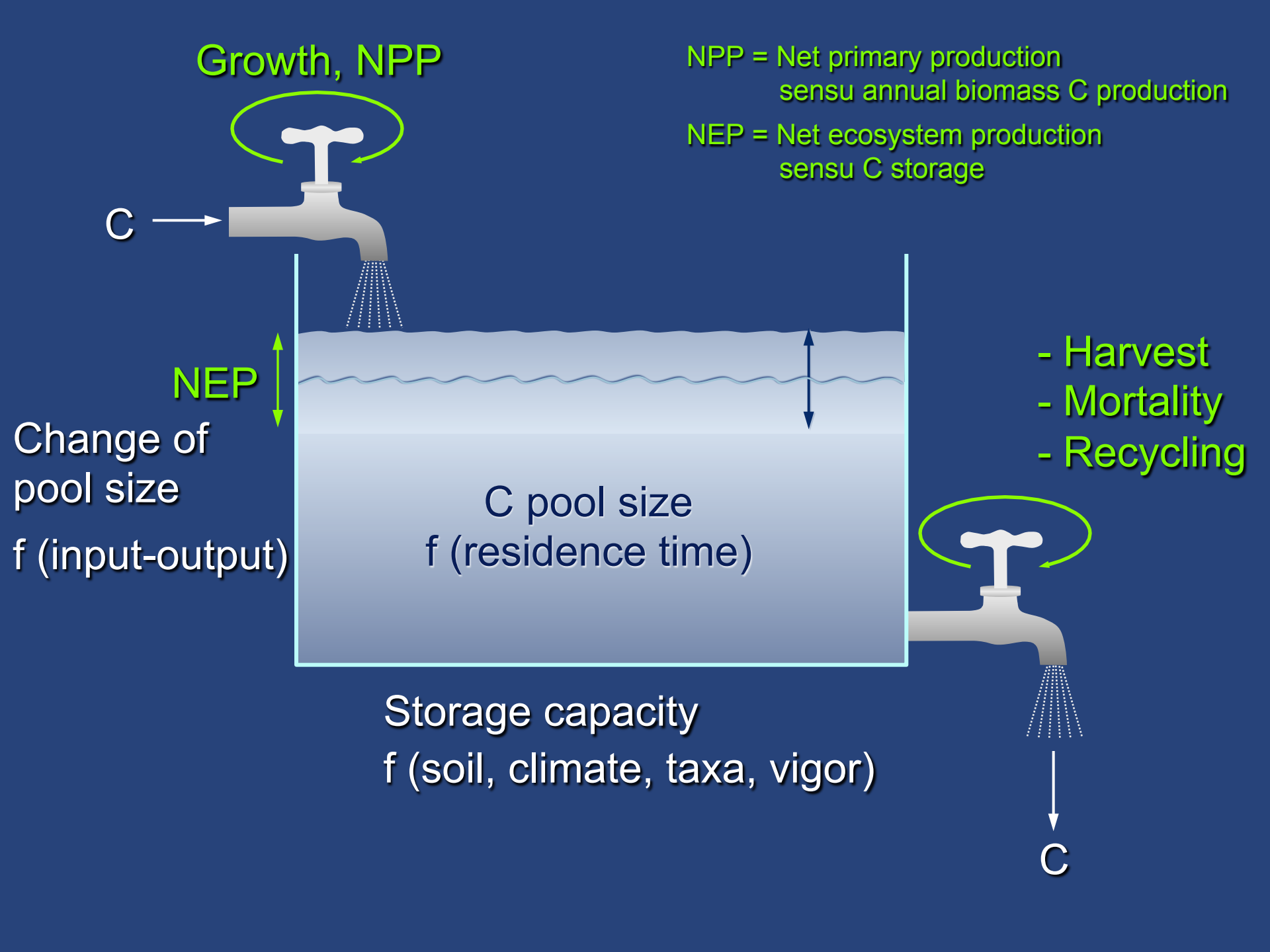
Change of
pool size
f (input-output)

C pool size
f (residence time)

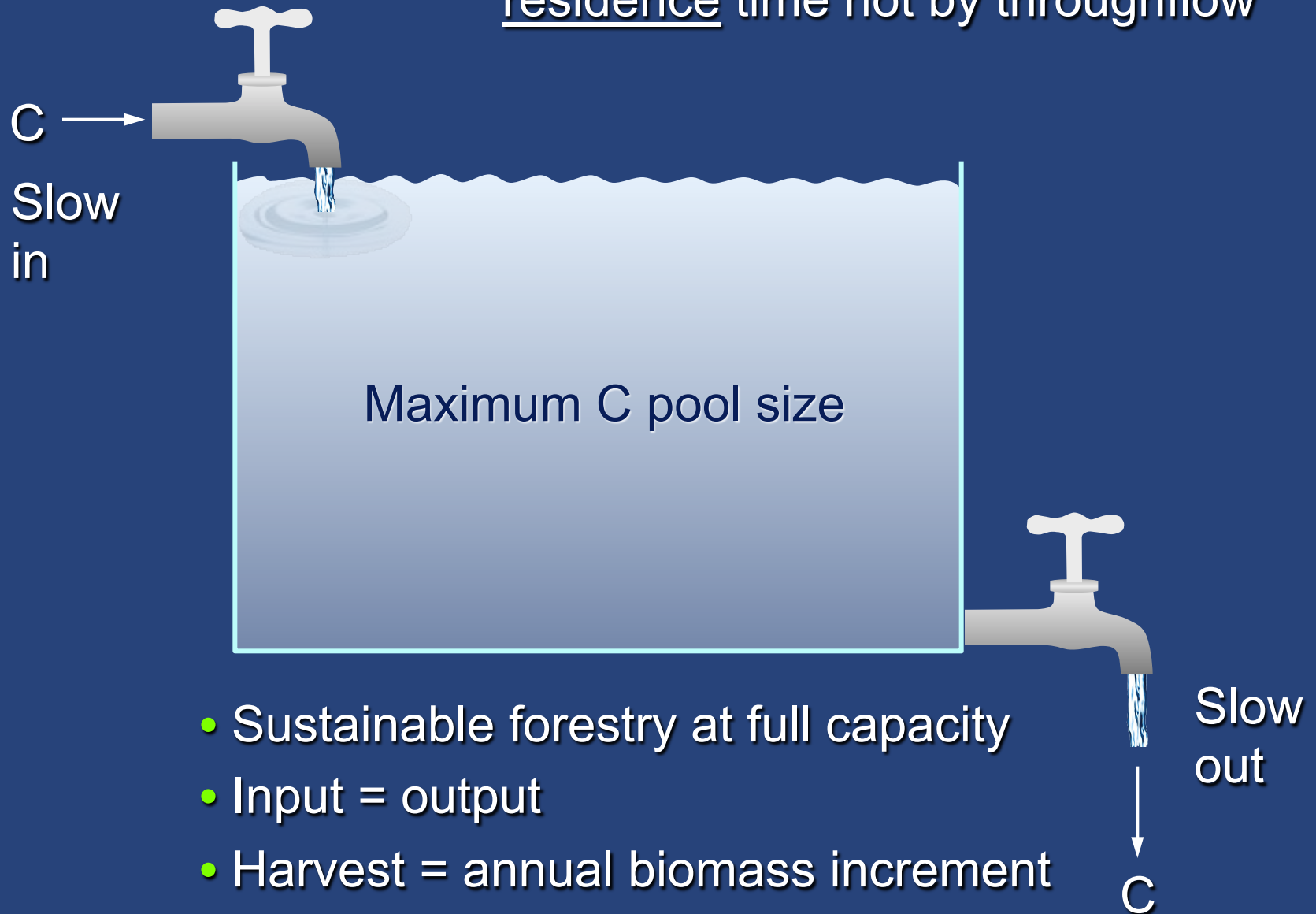
Storage capacity
f (soil, climate, taxa, vigor)

- Harvest
- Mortality
- Recycling

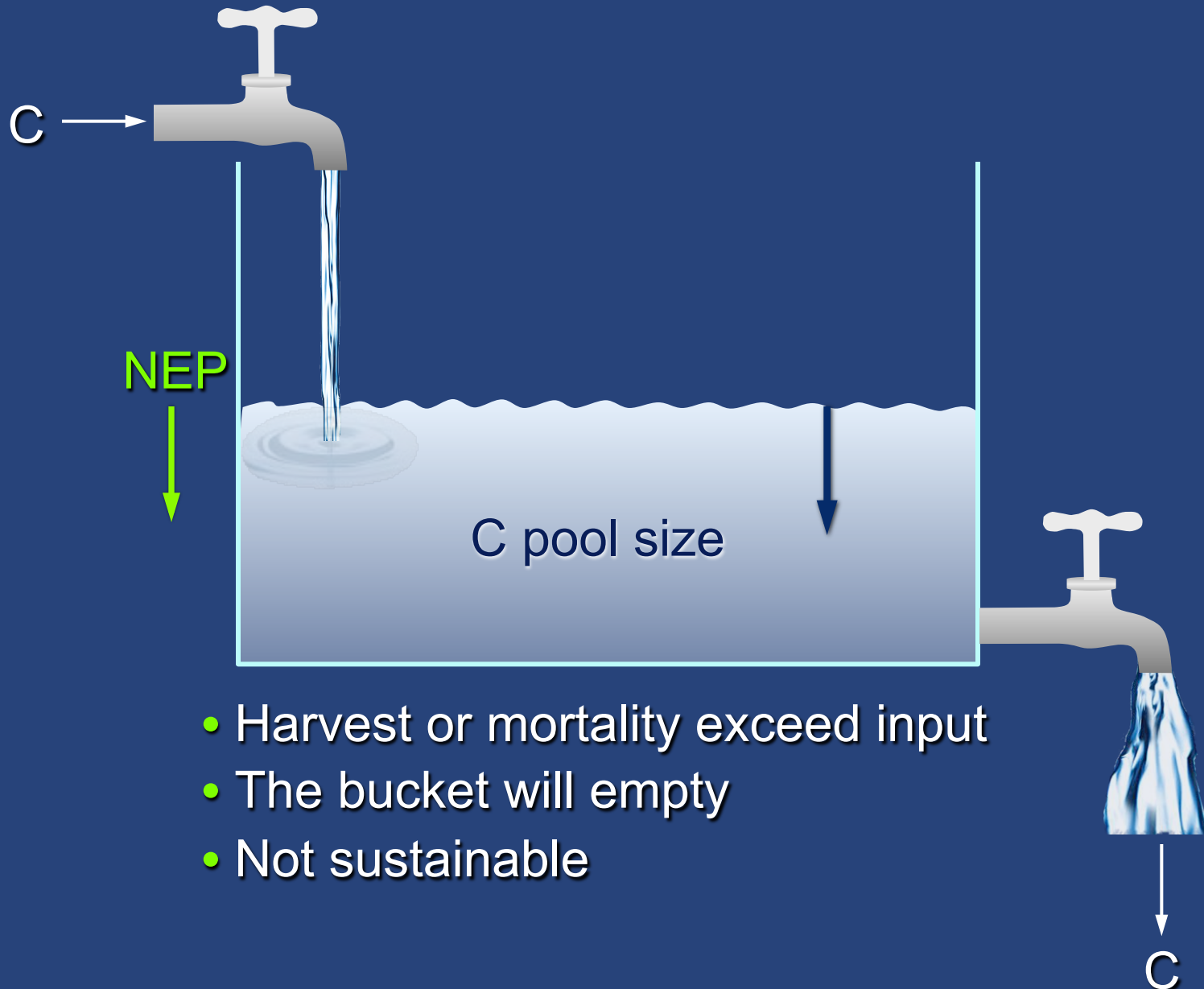
C



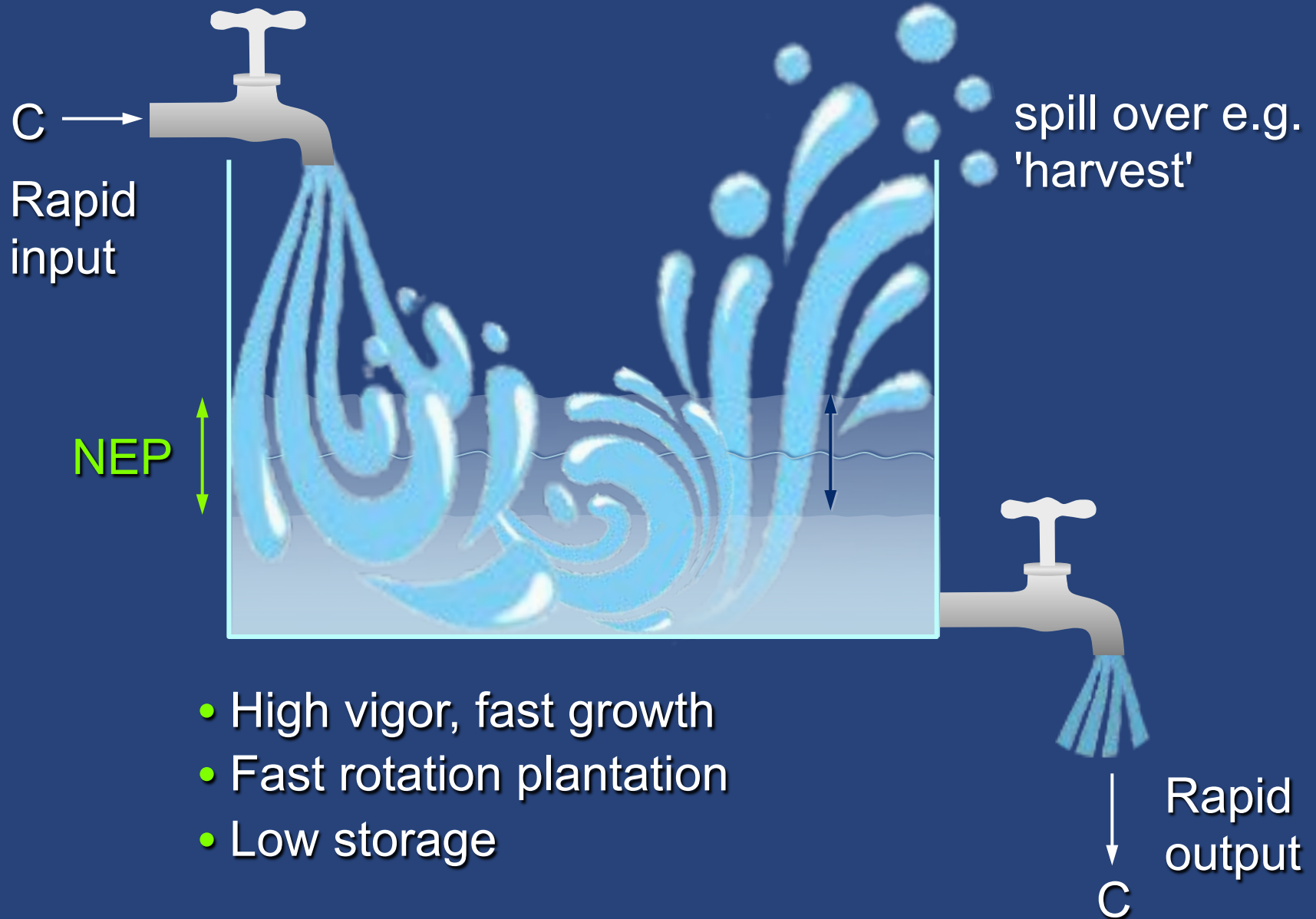
Storage is determined by residence time not by throughflow



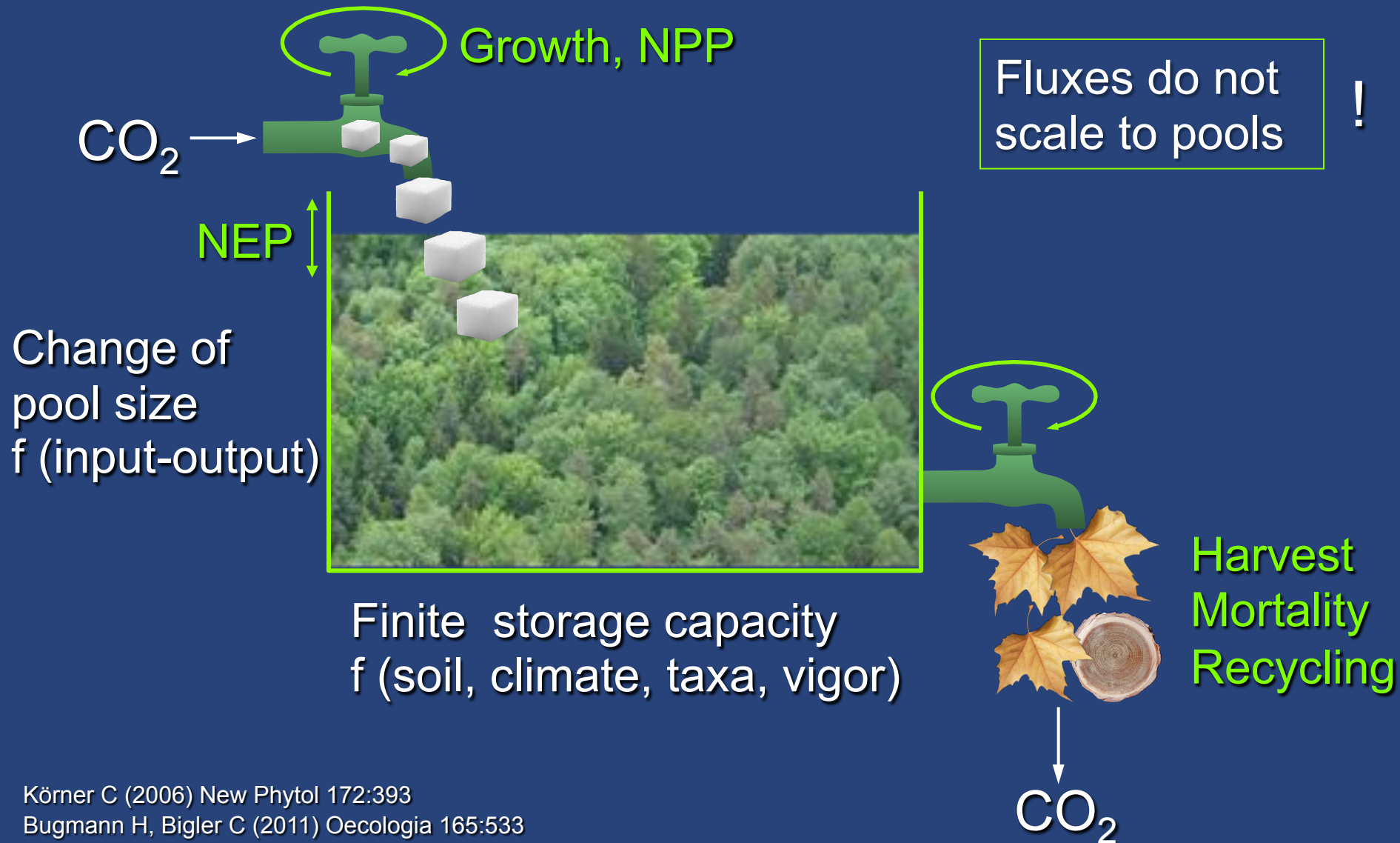
Negative C-balance



Productivity and storage are correlated negatively



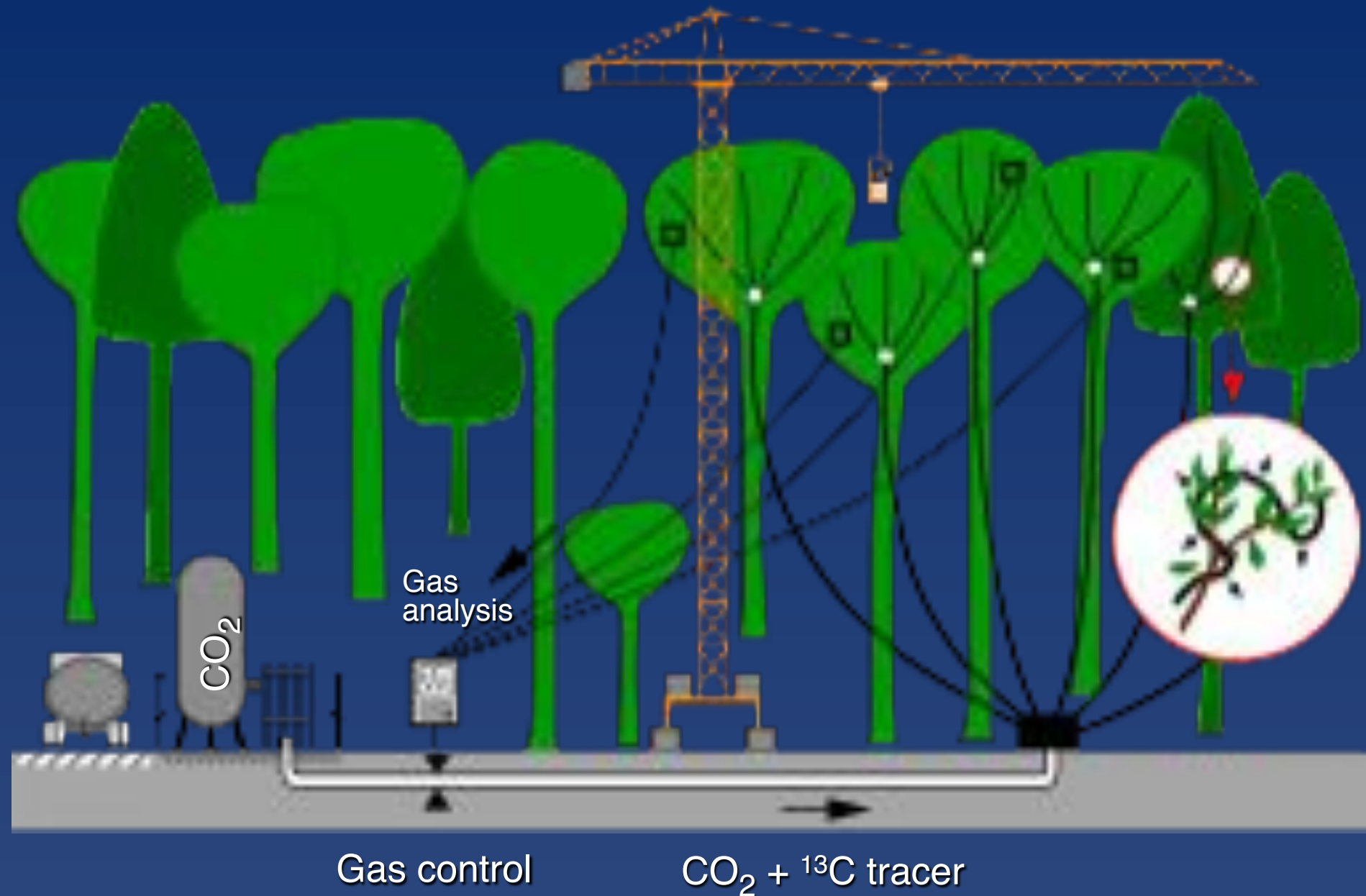
The C-capital (storage) is controlled by tree demography (residence time of C)



Is carbon a limiting resource?

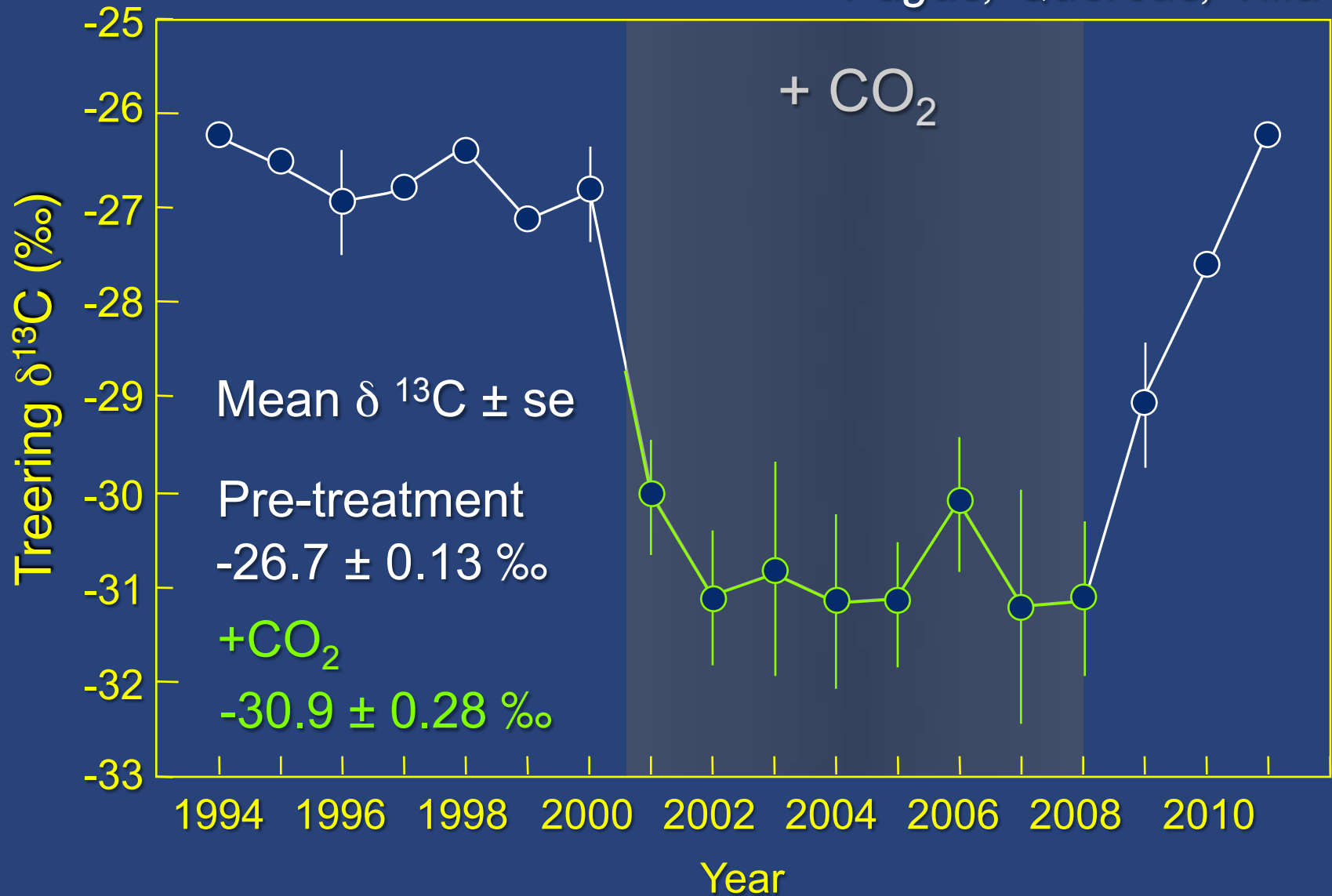


web-FACE at the Swiss Canopy Crane site

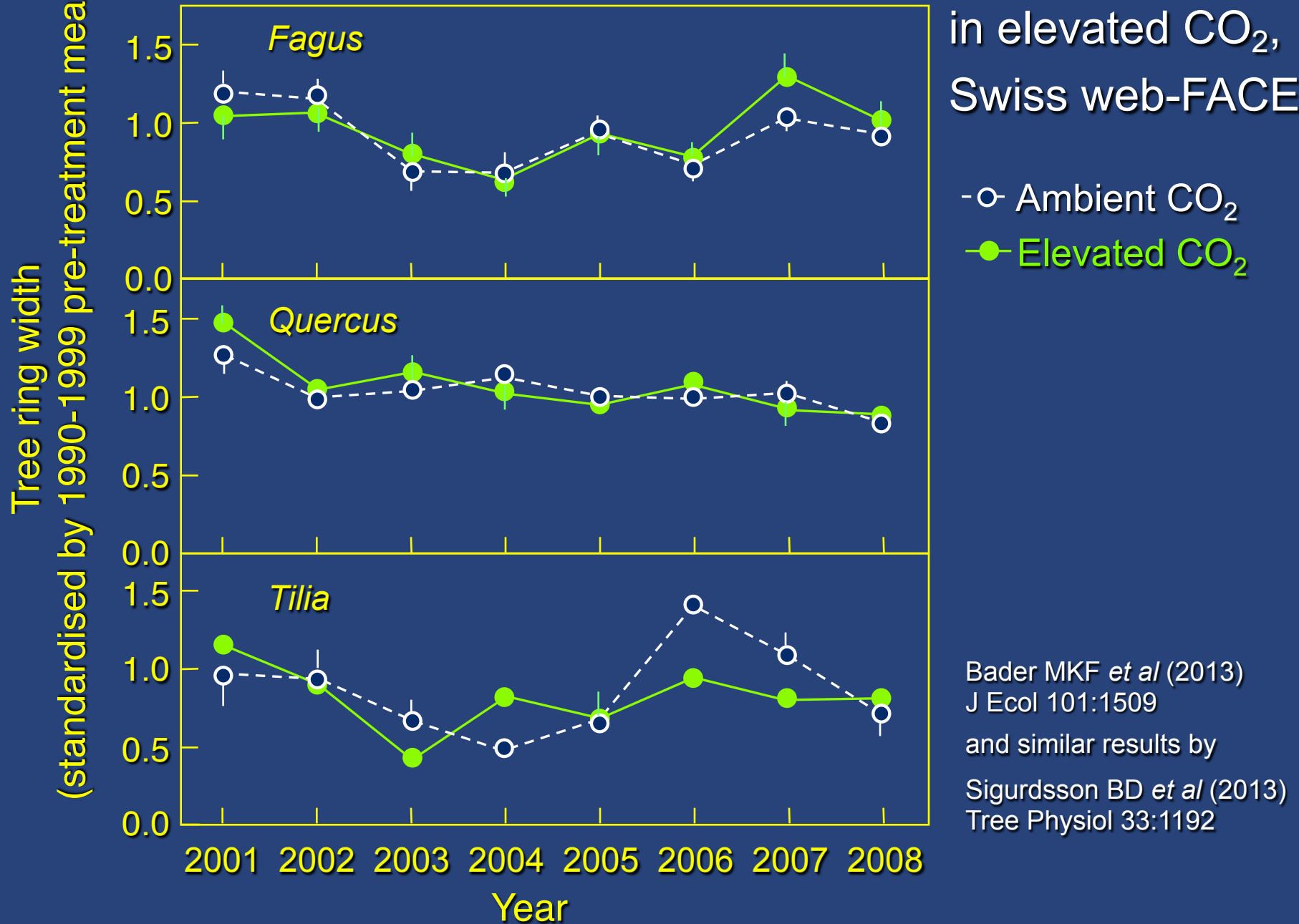


^{13}C isotopic signal

Fagus, Quercus, Tilia



... Not as rated by growth of 100 year old trees
in elevated CO₂,
Swiss web-FACE



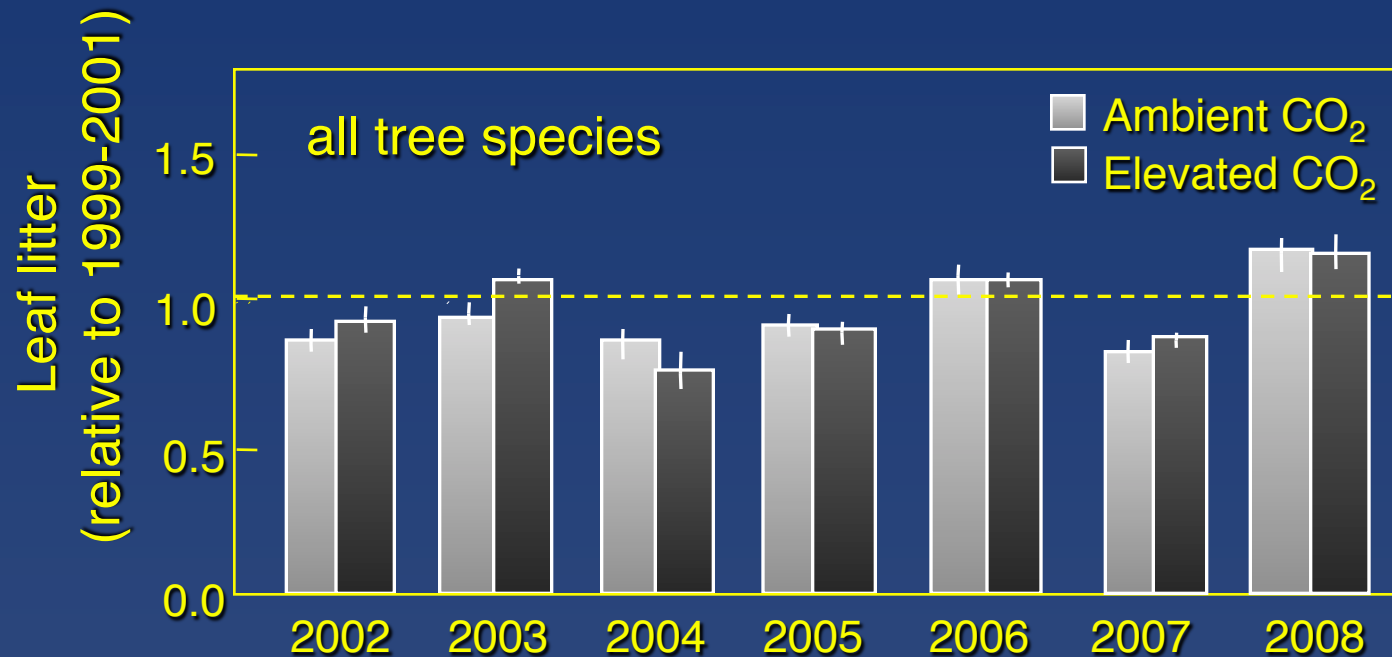
Bader MKF *et al* (2013)
J Ecol 101:1509

and similar results by

Sigurdsson BD *et al* (2013)
Tree Physiol 33:1192



... not as rated by
leaf litter production



No change
in allocation
to leaves
(and fine roots)

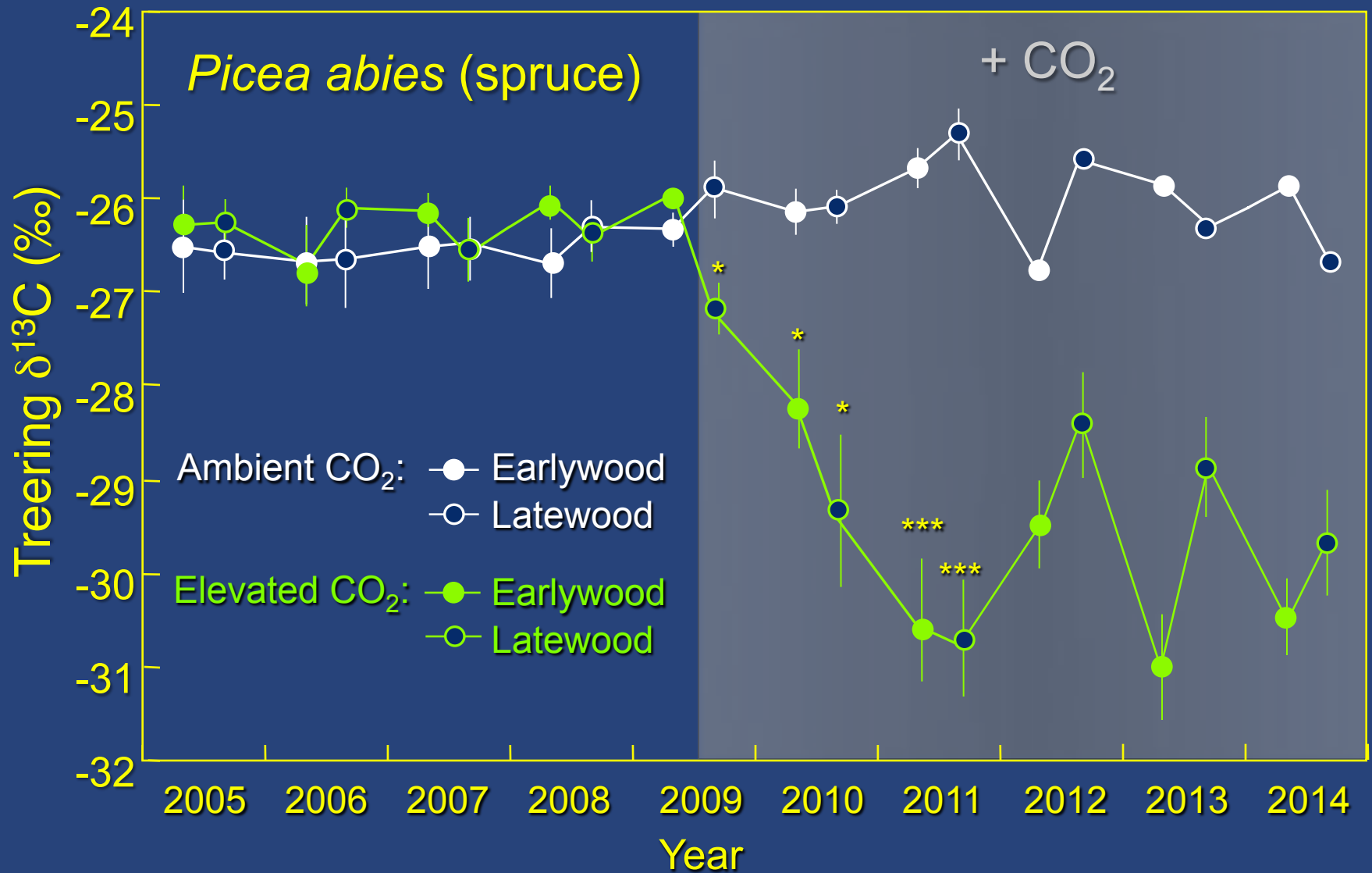
Körner C *et al* (2005)
Science 309:1360

Bader MKF *et al* (2013)
J Ecol 101:1509

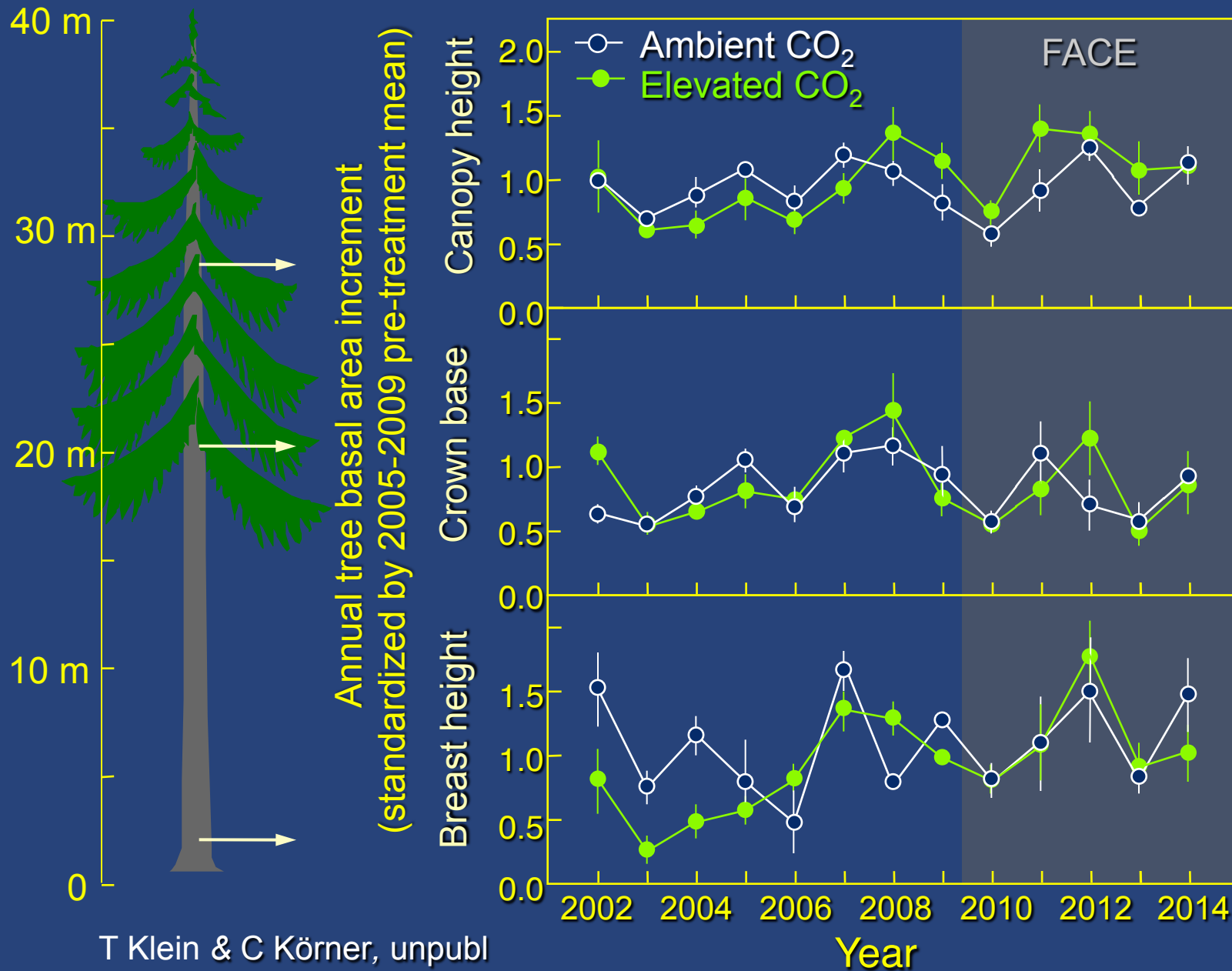
37 m tall spruce trees near Basel



^{13}C isotopic signal



Growth effects of elevated CO₂ on *Picea abies*



Summary on elevated CO₂

- Commonly, assumed first principle responses (e.g. photosynthetic, respiratory or stomatal responses) don't scale.
- The rate of tissue formation controls the rate of carbon capture.
- Tissue formation is controlled by the most limiting resource which commonly is not C in a 400 ppm world.



Climate driven range limits of trees

Treeline



- The high elevation and high latitude tree limit, the treeline, is a lifeform limit.
- Several species may occupy it.

Tree species limit



- All species have a species specific low temperature limit.
- Each species has its own limit.

Warming affects both.

ERC - TREELIM: Tree species cold limits what - where - why?

Biogeography and climatology

Realized
niche &
macro-
climate
(GIS)

Elevation
vs.
latitude

True
climate:
Micro-
climatology
(cross-
continental
data
logging)

Hindcasting
past climate
and extreme
events

Population processes and Evolution

Repro-
ductive
potential
(seeds &
viability)

Population
dynamics &
recruitment
(demo-
graphy)

Evolutio-
nary
adaptation
(reciprocal
common
garden)

Seedling
growth

Dispersal
limitation

Biometric
traits

Phenology

Growth and stress physiology

Freezing
resistance

Growth
dynamics
& carbon
relations

In situ
adult
tree
growth
(dendro-
logy)

Phytotron
experi-
ments
(carbo-
hydrates,
nutrients)

Biogeography Species range limits

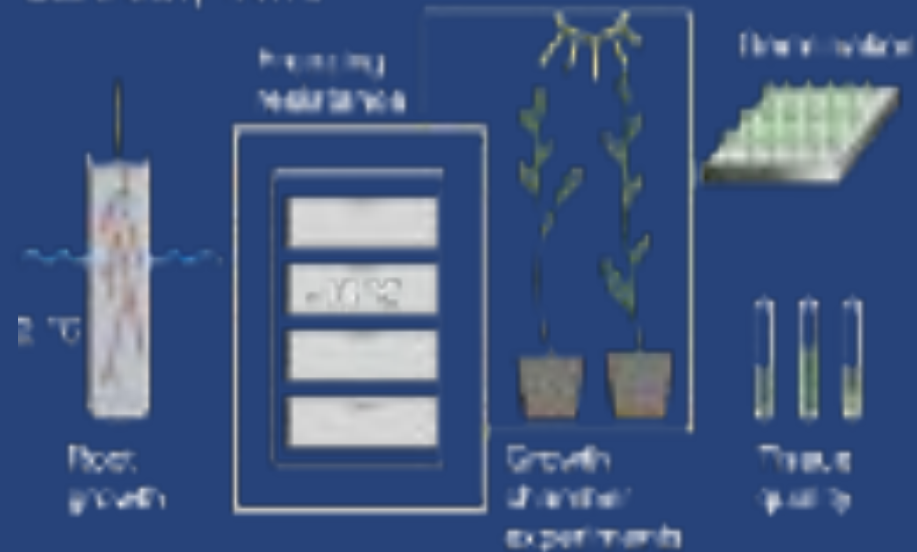
- Latitude
- Elevation



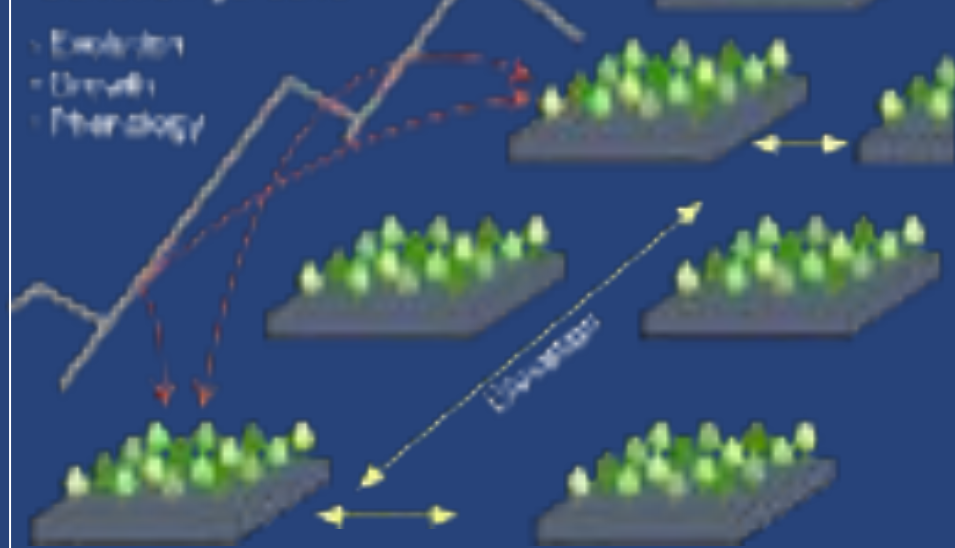
Field studies along elevation transects



Laboratory works



Common gardens



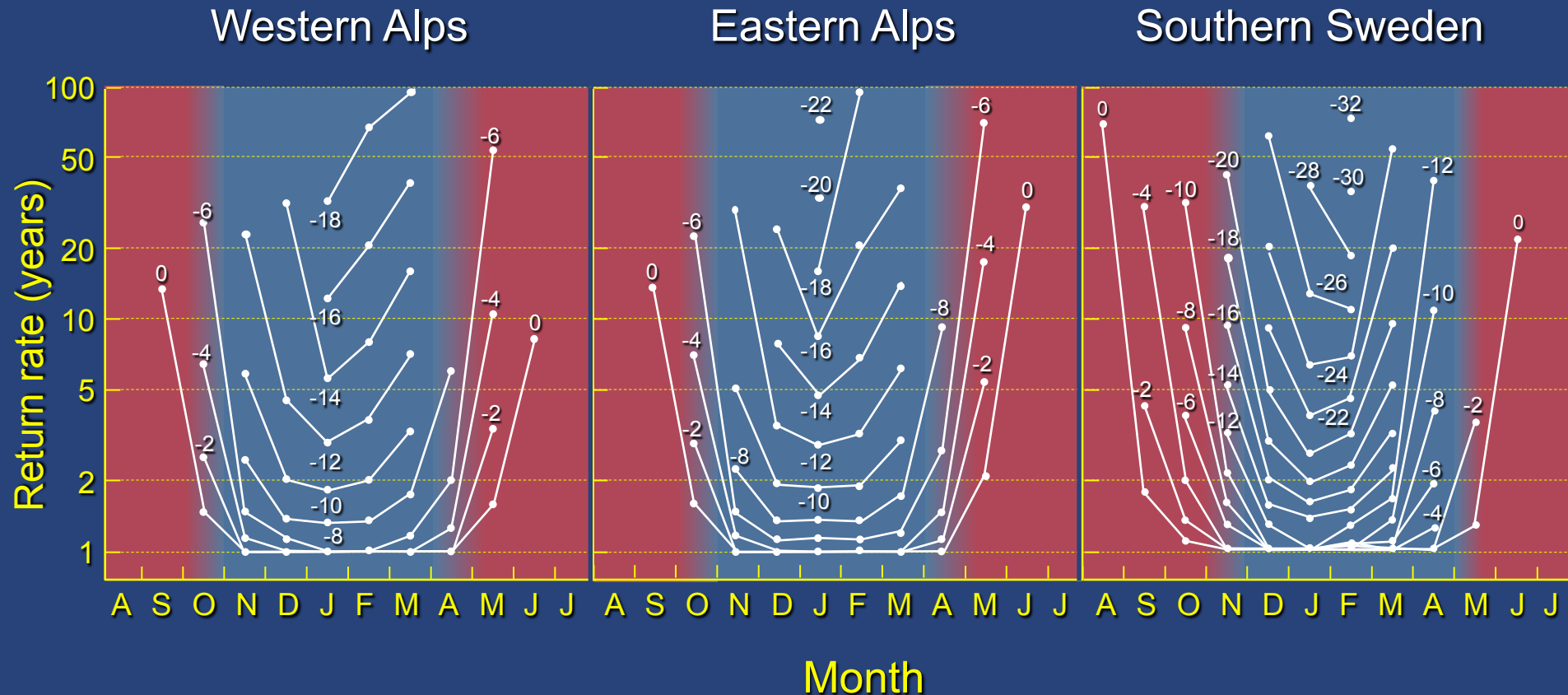
Night time minima of temperature in the top of tree crowns



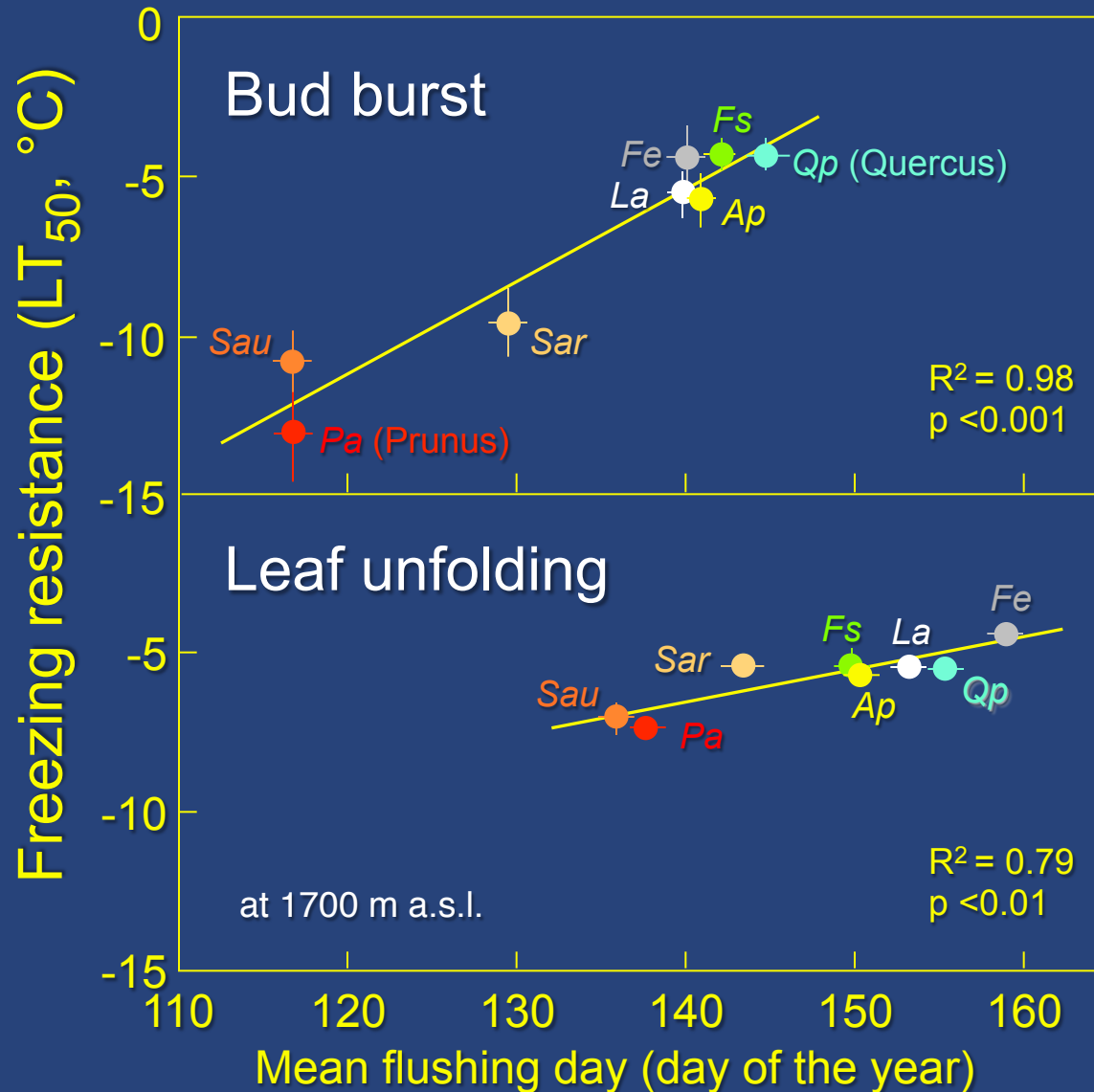
... match weather station records by 0.5 K

Return rates of extreme temperatures

Lowest temperatures (°C) predicted to occur during 100 years at the species limit of *Prunus avium*, as an example

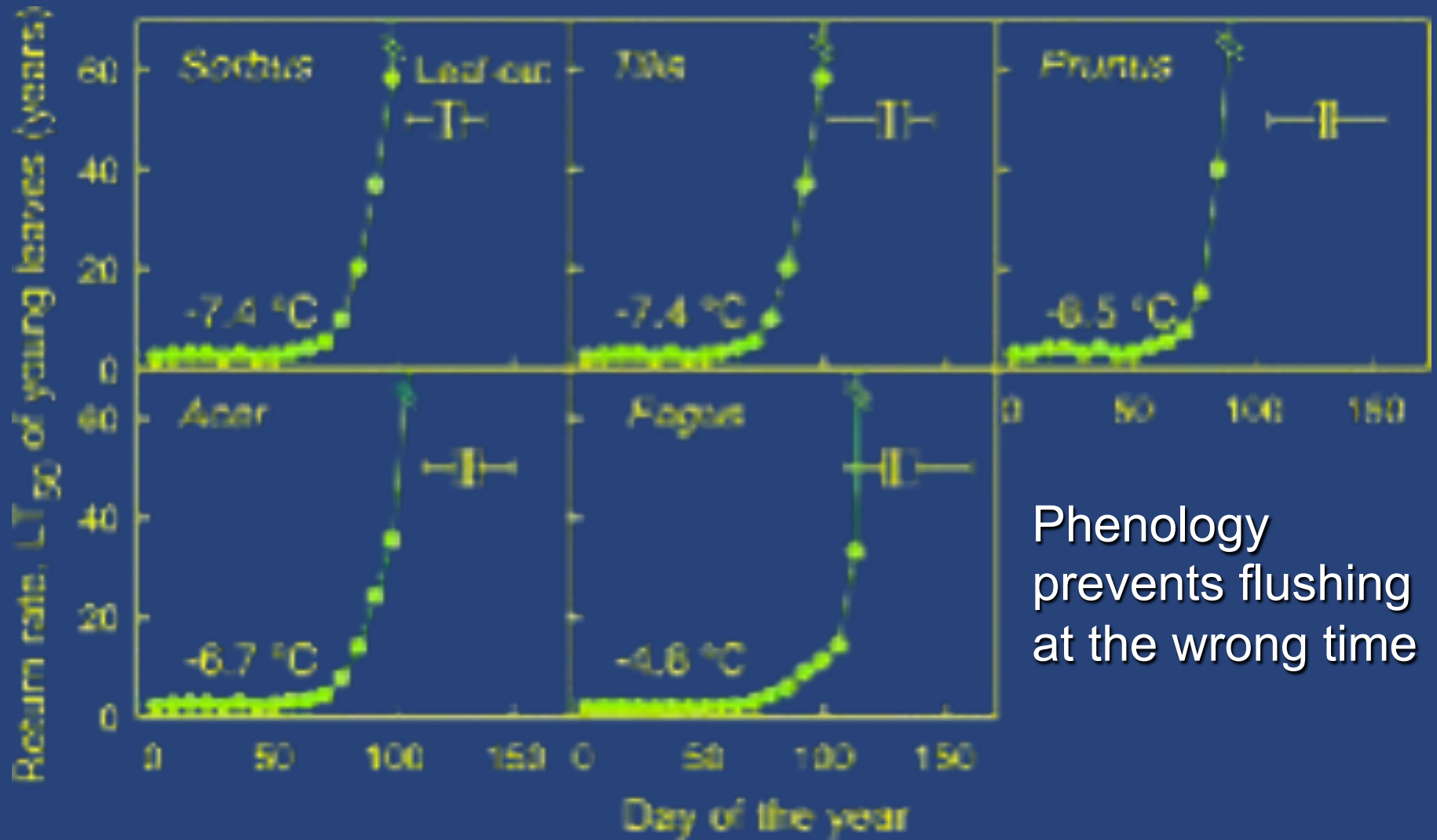


Freezing resistance during dehardening in spring



Early flushing species are more resistant than late flushing species

Risk of freezing damage in young leaves



Phenology
prevents flushing
at the wrong time

Controls of tree phenology in spring

- Opportunistic (T-only)



Syringa

- Chilling
- Temperature



Carpinus

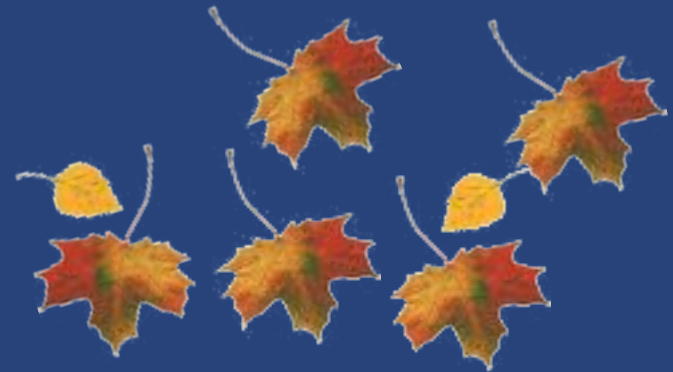
- Chilling
- Photoperiod
- Temperature



Fagus

End of season phenology

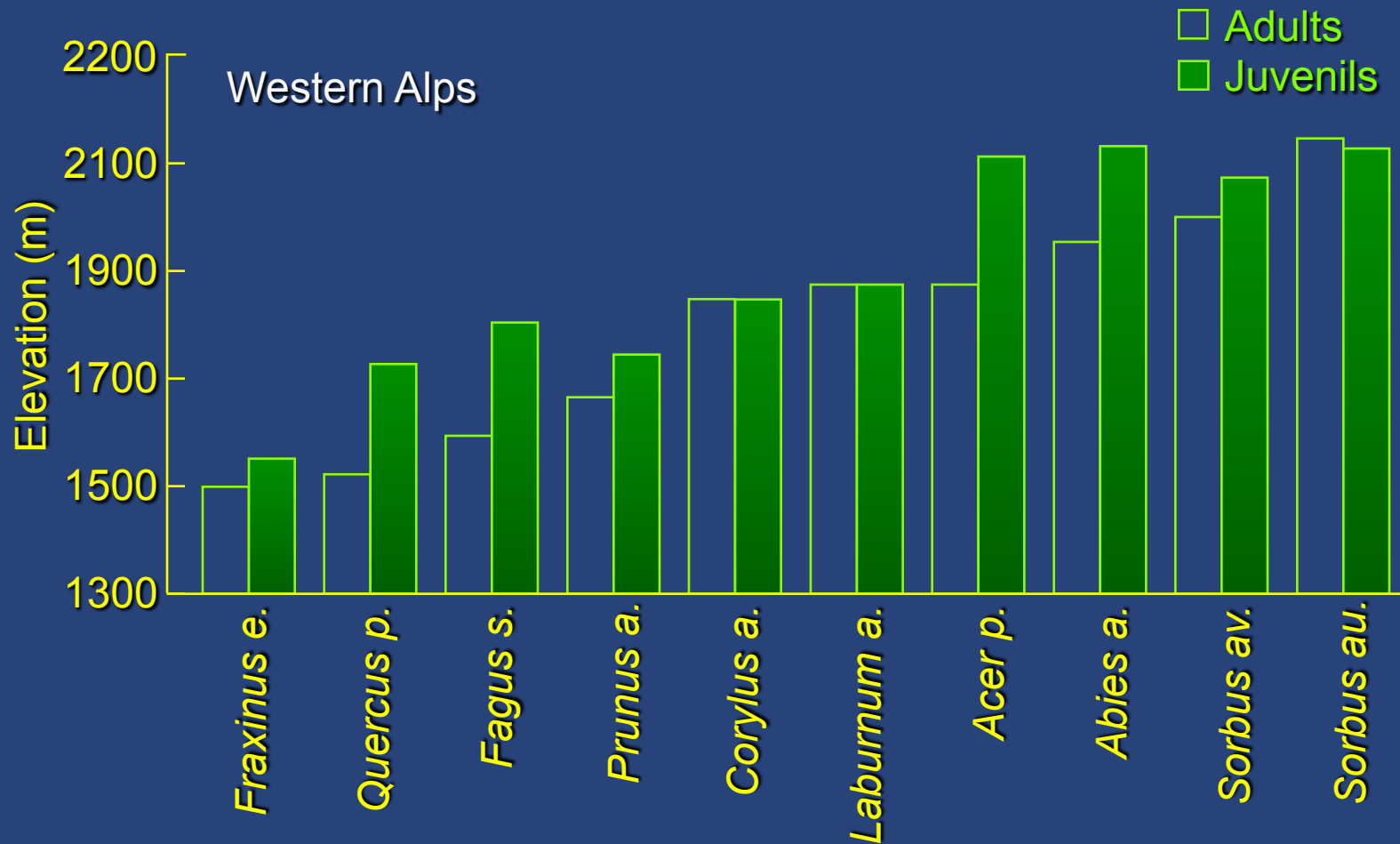
Leaf coloration is misleading



- A longer season as rated by eye (phenology), should not be mistaken as an expression of the plant's internal state.
- The plant internal controls set developmental limits (time constraints).
- A longer greenness would only matter if there is C-limitation (no evidence).
- Autumnal phenology is driven by photoperiod.

Elevational limits of trees in the Alps:

Juvenile (seedlings and saplings) were found at and beyond the adult elevational limits



Kollas C *et al* (2012) *Ann Bot* 109:473

Vitasse Y *et al* (2012) *J Biogeogr* 39:1439

Summary on range limits of trees and phenology

Tree species limits below treeline are set by

- Phylogenetic maximum **freezing tolerance** in spring
- **Phenology** is the way to escape dangerous freezing events but this constrains the length of the growing season.
- Phylogenetic life history traits define a minimum **season length** (e.g. tissue maturation, seed ripening).

Short term

Long term

Short term

Spring
effects

Micro-evolution

Winter
effects

Losses of
immature
tissue

Phenology
of
bud break

Losses of
immature
tissue

Minimum
season
length

Maximum freezing
resistance in
spring

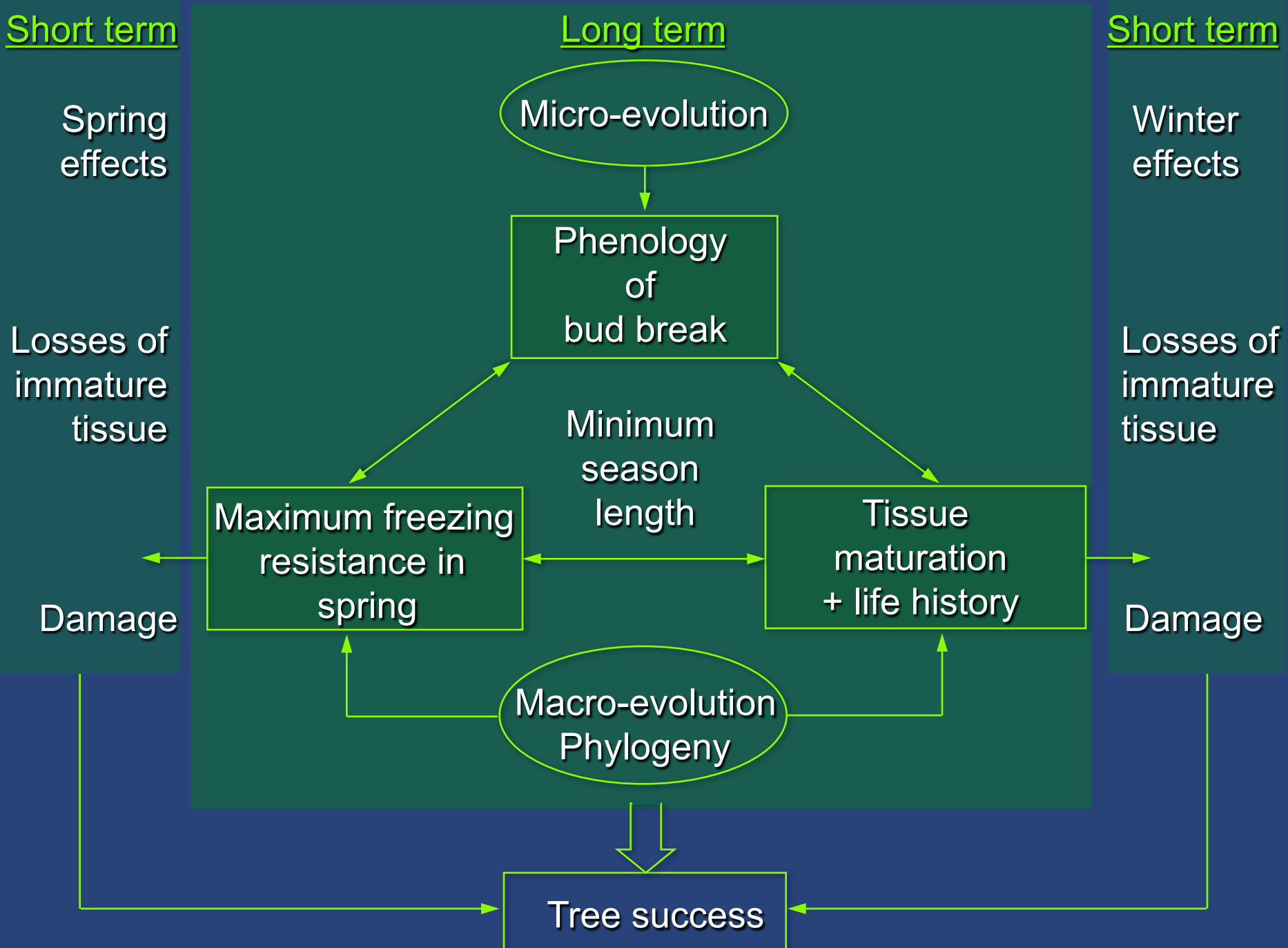
Tissue
maturation
+ life history

Damage

Damage

Macro-evolution
Phylogeny

Tree success



The 'Treelim core team'



European
Research
Council



From left to right:
Christian Körner, Chris Kollas, Christophe Randin, Armando Lenz, Günter Hoch, Yann Vitasse

Overall conclusions

- Carbon sinks control C sources (mostly).
- Forest productivity is not C limited.
- C sequestration in forests requires a longer residence time of C in biota (tree turnover, tree demography).
- Tree phenology is an issue of stress tolerance in interaction with developmental constraints (not related to carbon relations).



... the more older trees the more carbon