Understanding drought stress in trees

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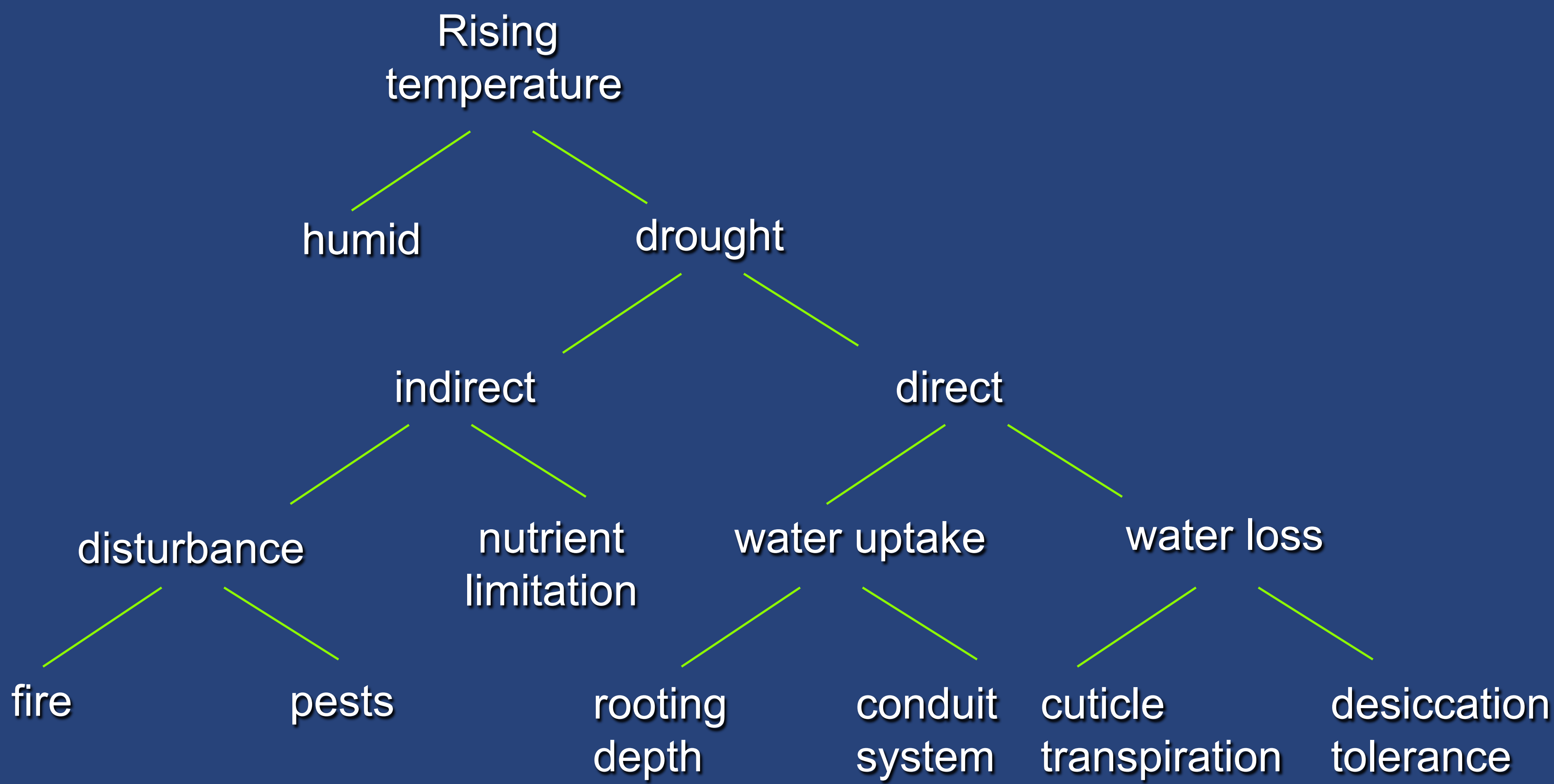
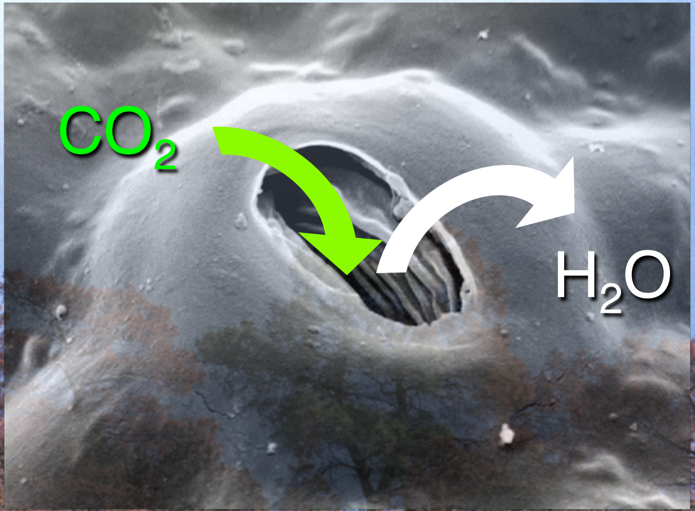
The action of drought on trees



Tree species differ in traits and sensitivites

Classical view at the consequences of water shortage



Prevention of water loss at the price of CO_2 shortage

Is there a role for **carbon**?

Yes – if drought duration exceeds the duration
of accessible C-reserves
- it very rarely does

No – if desiccation occurs before C starvation
becomes an issue
- the common case

Is there a role for **nutrients**?

Yes – if new tissue formation is prevented
- rarely an issue, because growth is halted

No – if internal allocation can match needs (e.g. for fine root growth)
- the common case


The carbon centric view of plant growth rests on the availability of excellent tools
... but it lacks on empirical foundation outside horticultural growth conditions
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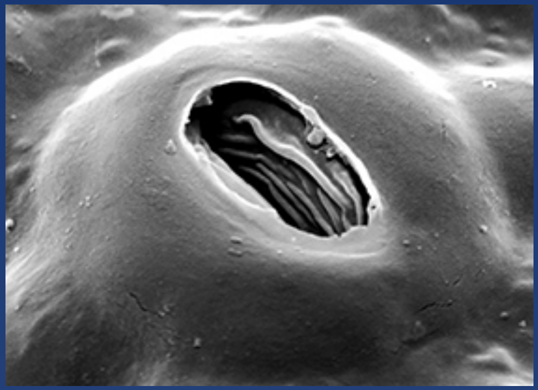
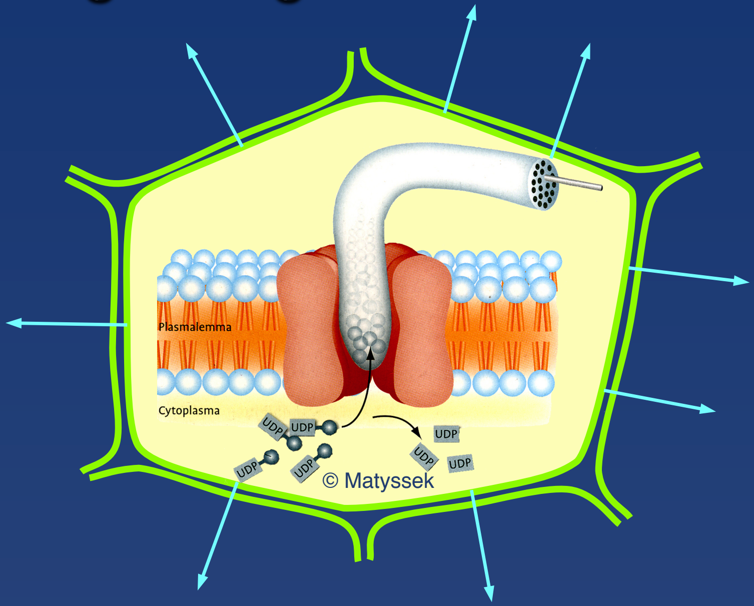
Drought: sinks are affected first

Water shortage:

Old	New
Stomatal closure and inhibition of photosynthesis	Turgor driven yielding of the cell wall in a growing cell ceases

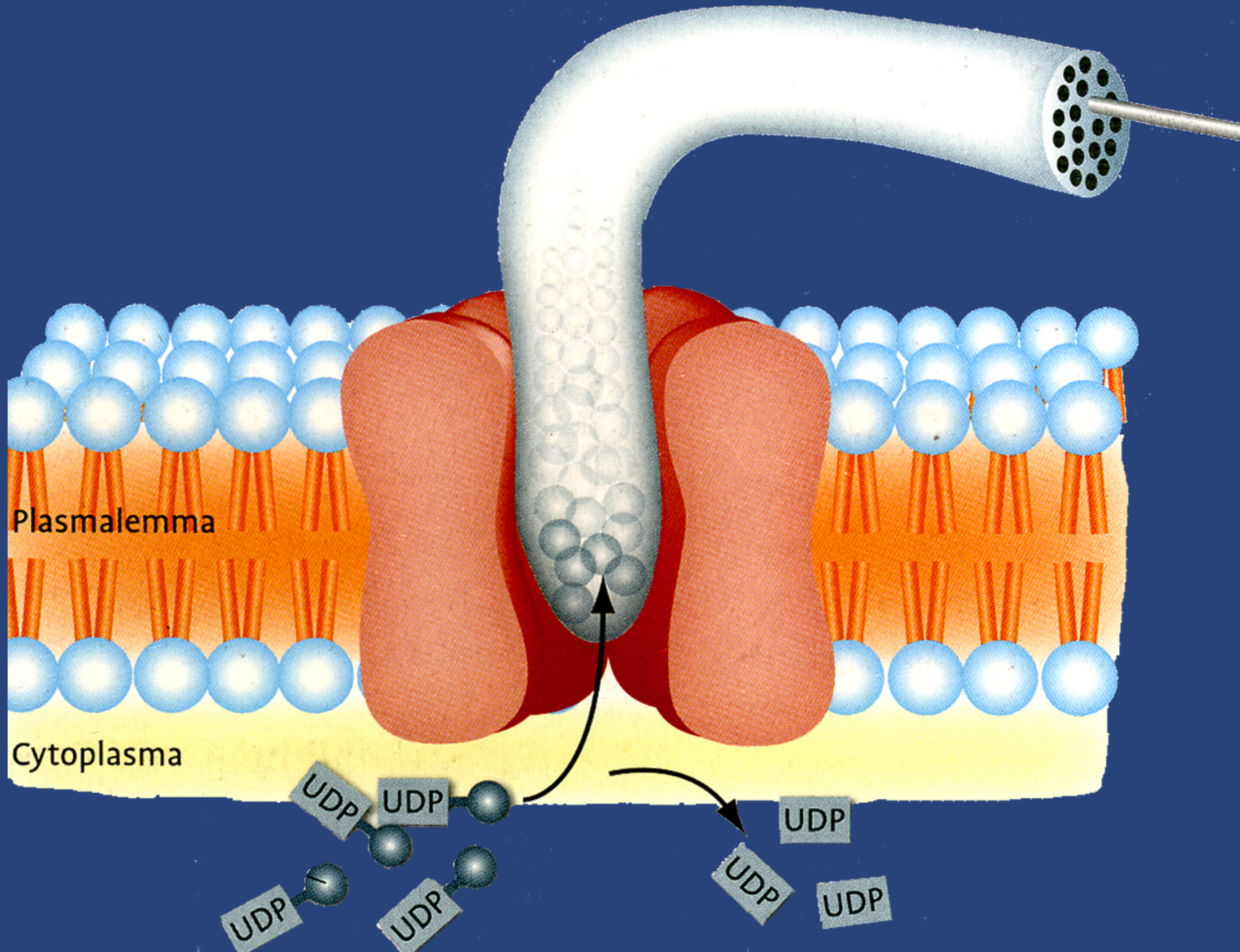




-1.2 to -2.0 MPa	-0.5 to -1.0 MPa
Source	Sink

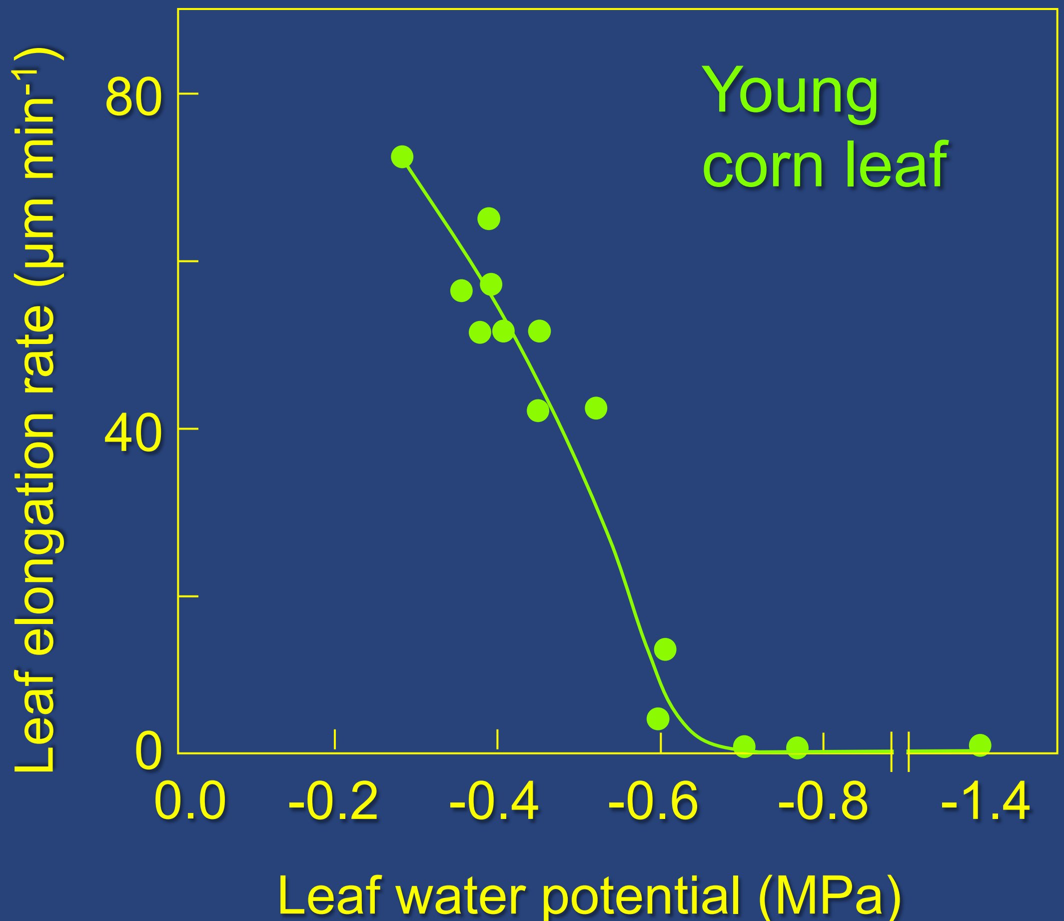
Körner C (2015) Curr Opin Plant Biol 25:107

→ Drought affects the balance between cell expansion (turgor) and cell wall growth



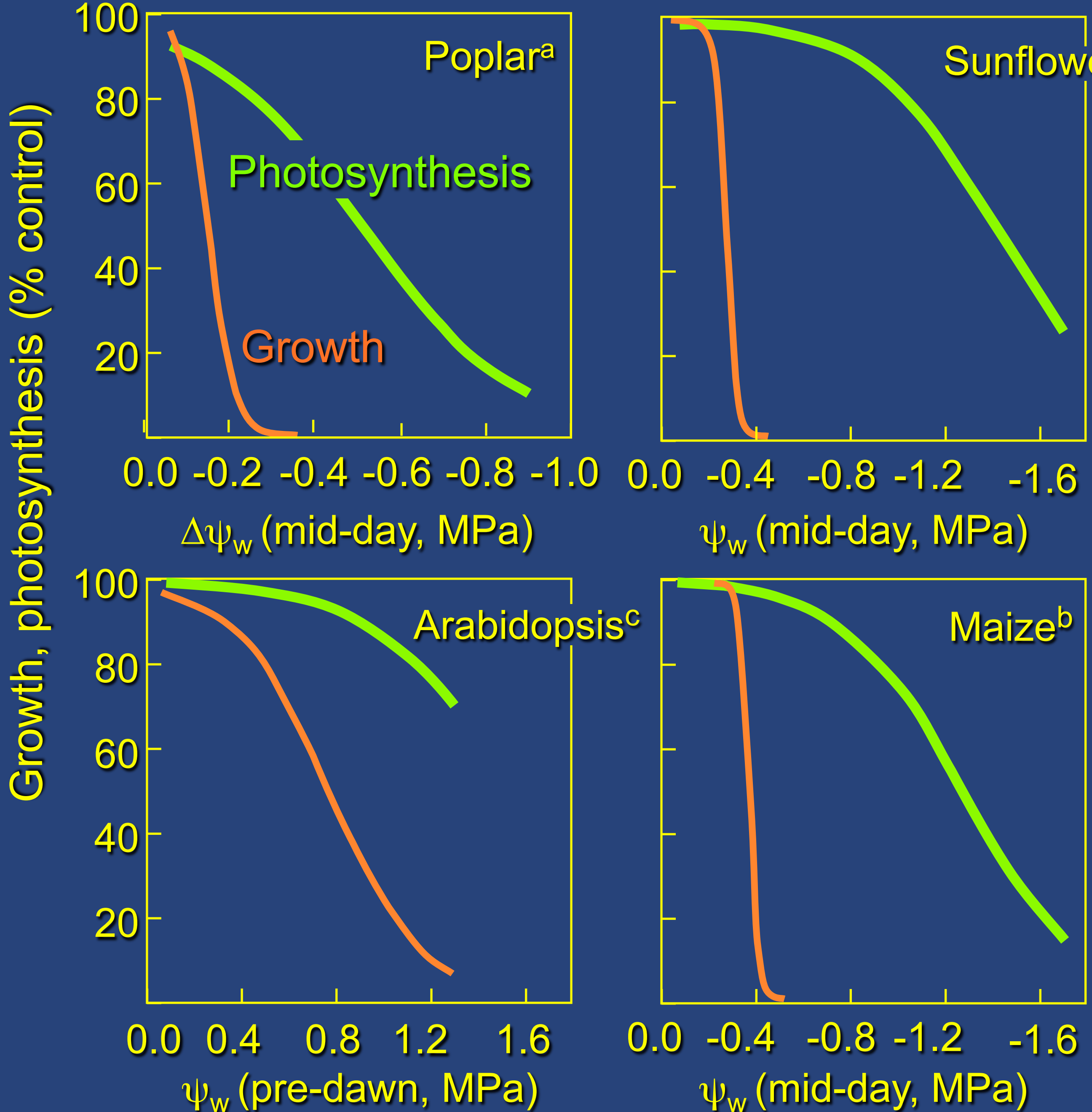
R Matyssek *et al* (2010) Biologie der Bäume. UTB, Stuttgart

Classics in crop science



In: TC Hsiao *et al* (1976) Ecol Studies 19:281

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)

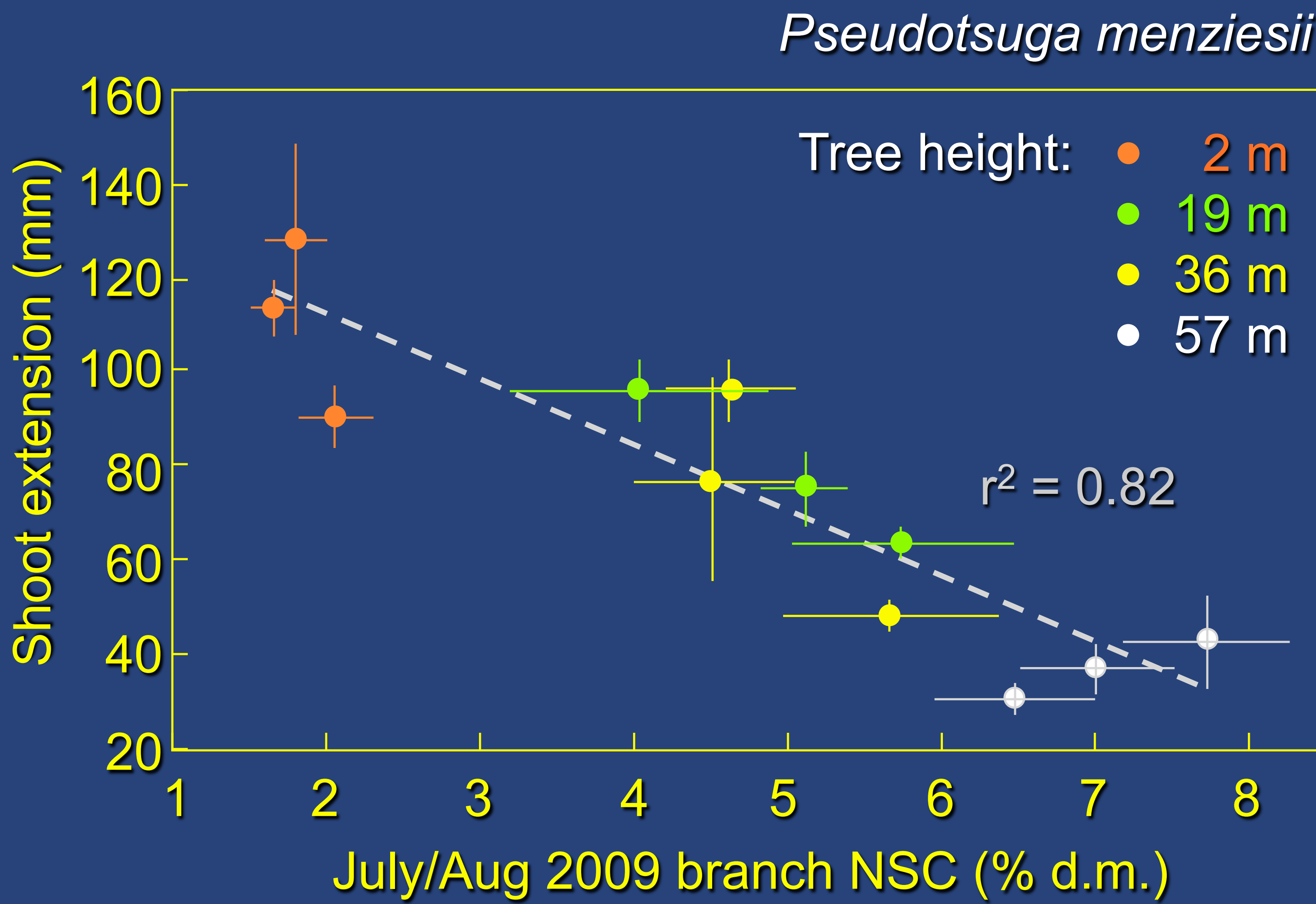
[c]Granier *et al* (2006), Hummel *et al* (2010)

Drought affects sinks first

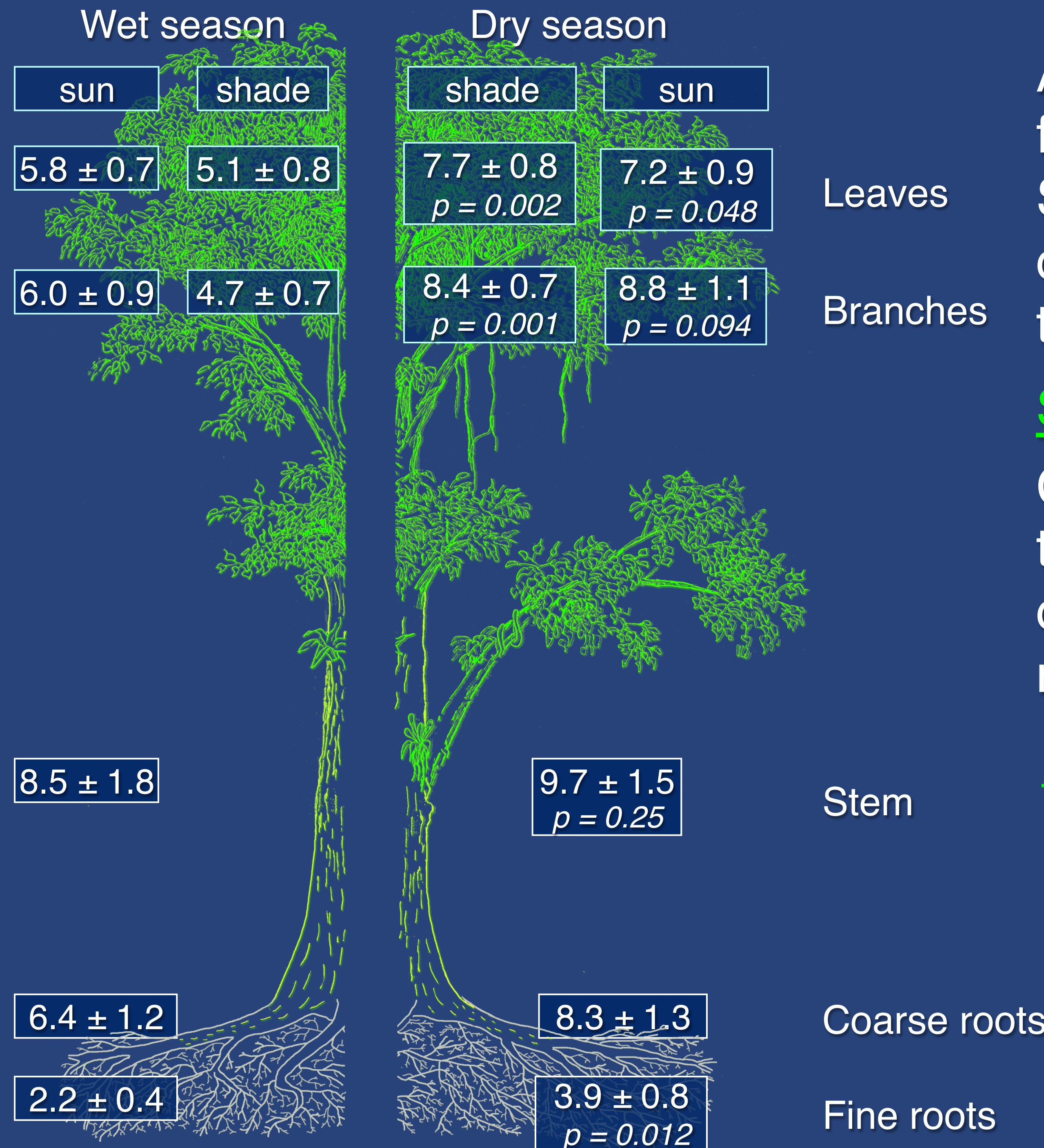
- Turgor driven cell wall yielding controls tissue formation.
- Carbohydrate transport is commonly not constrained, as evidence by the rise and fall of distant storage pools and ^{13}C tracer studies.
- Assimilate downloading and storage is always actively regulated; it ensures an operative photosynthetic machinery (e.g. prevention of photoinhibition).

\- Nothing is passive as long as plant is living.

A growth *vs.* storage trade off, irrespective of tree age



D Woodruff & F Meinzer (2011) PCE 34: 1920



A whole mature forest in Panama: Seasonal variation of NSC in tropical trees

<u>Sink limitation:</u>

Carbon allocation to reserves when drought constrains meristems

→ NSC ↑

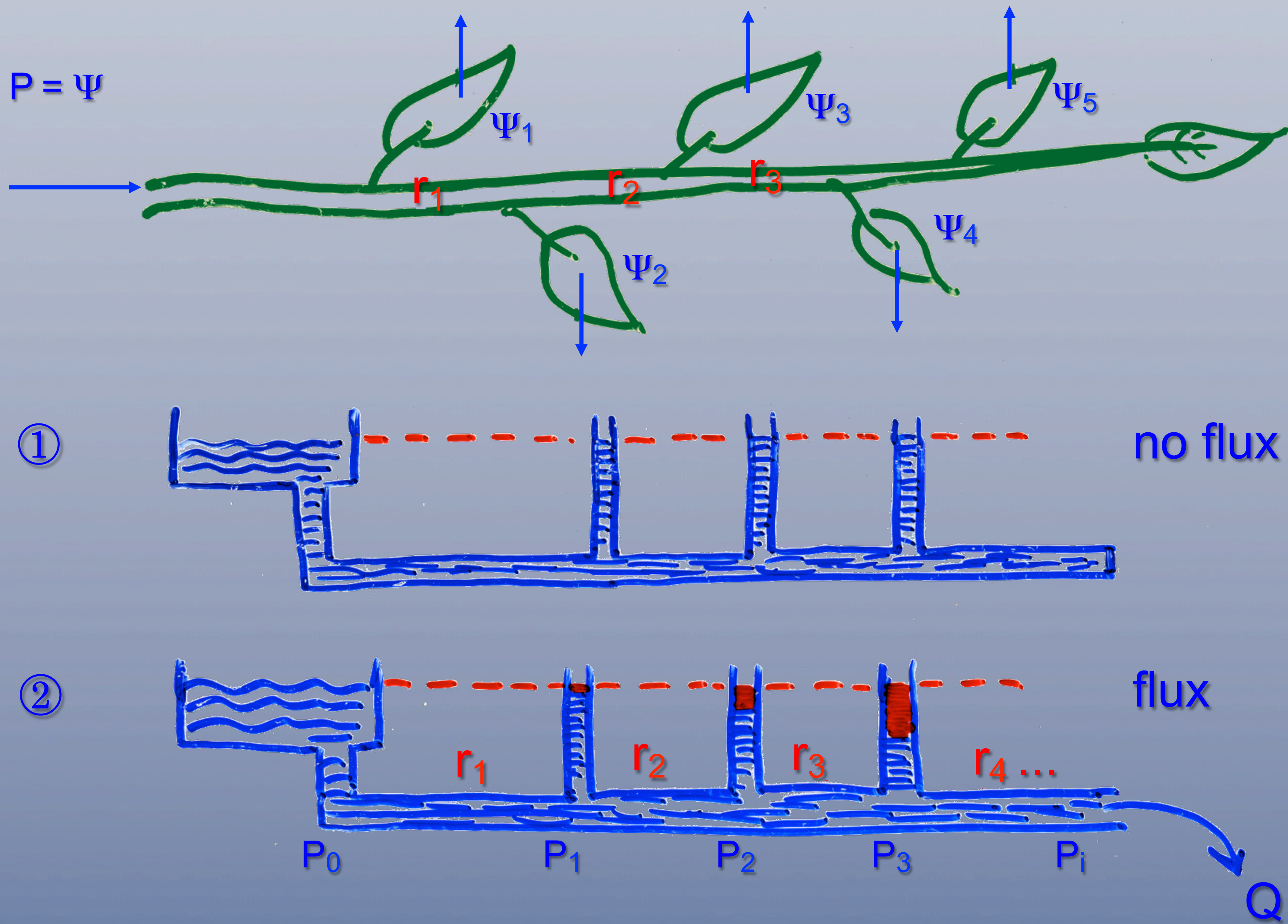
Würth M *et al* (2005)
Oecologia 143:11

Some basics of water plant relations:

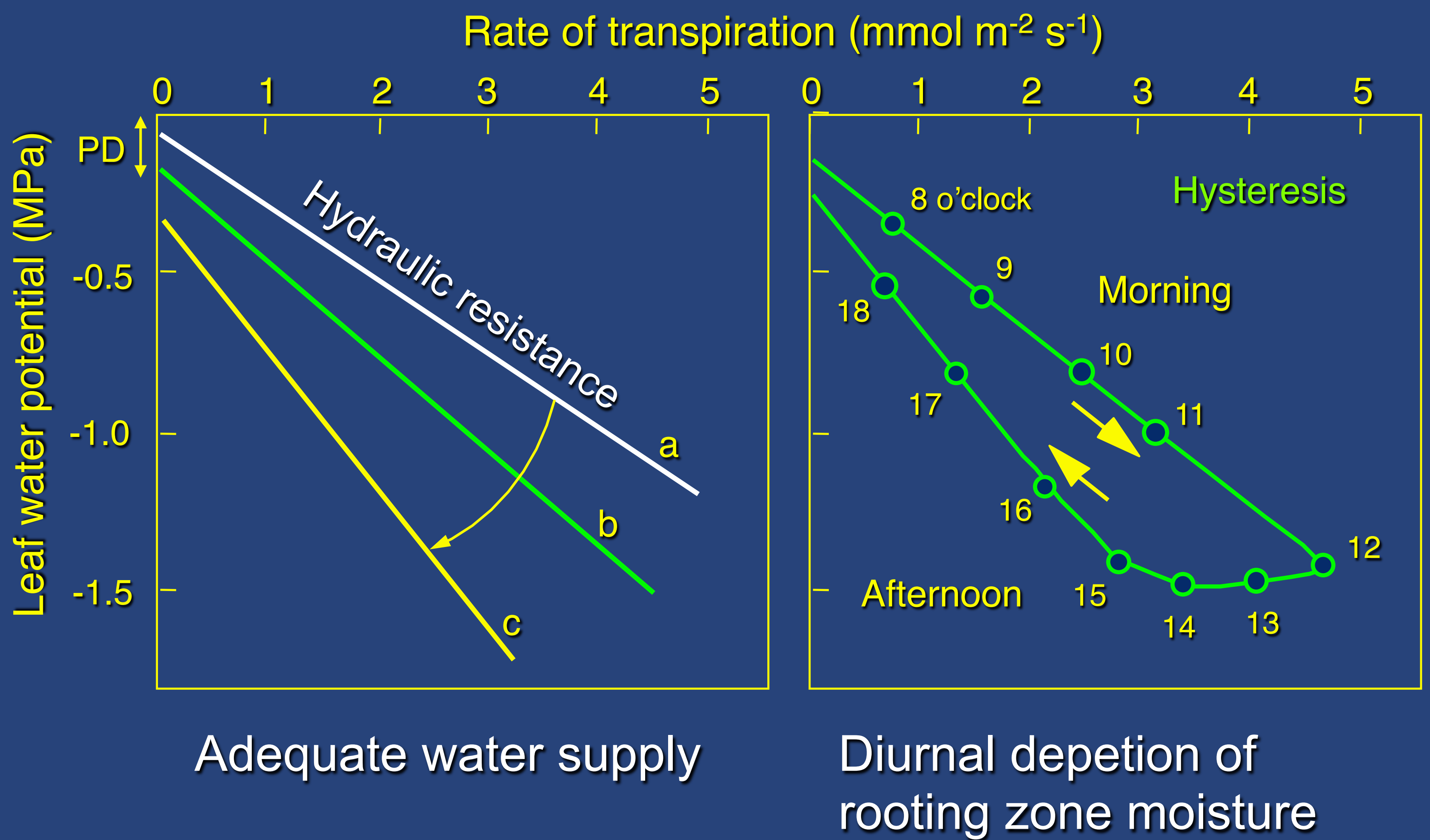
What is the pressure chamber measuring?

→ NOT xylem water potential!

A hydraulic analogue to a shoot



Flux drives water potential, not the other way round



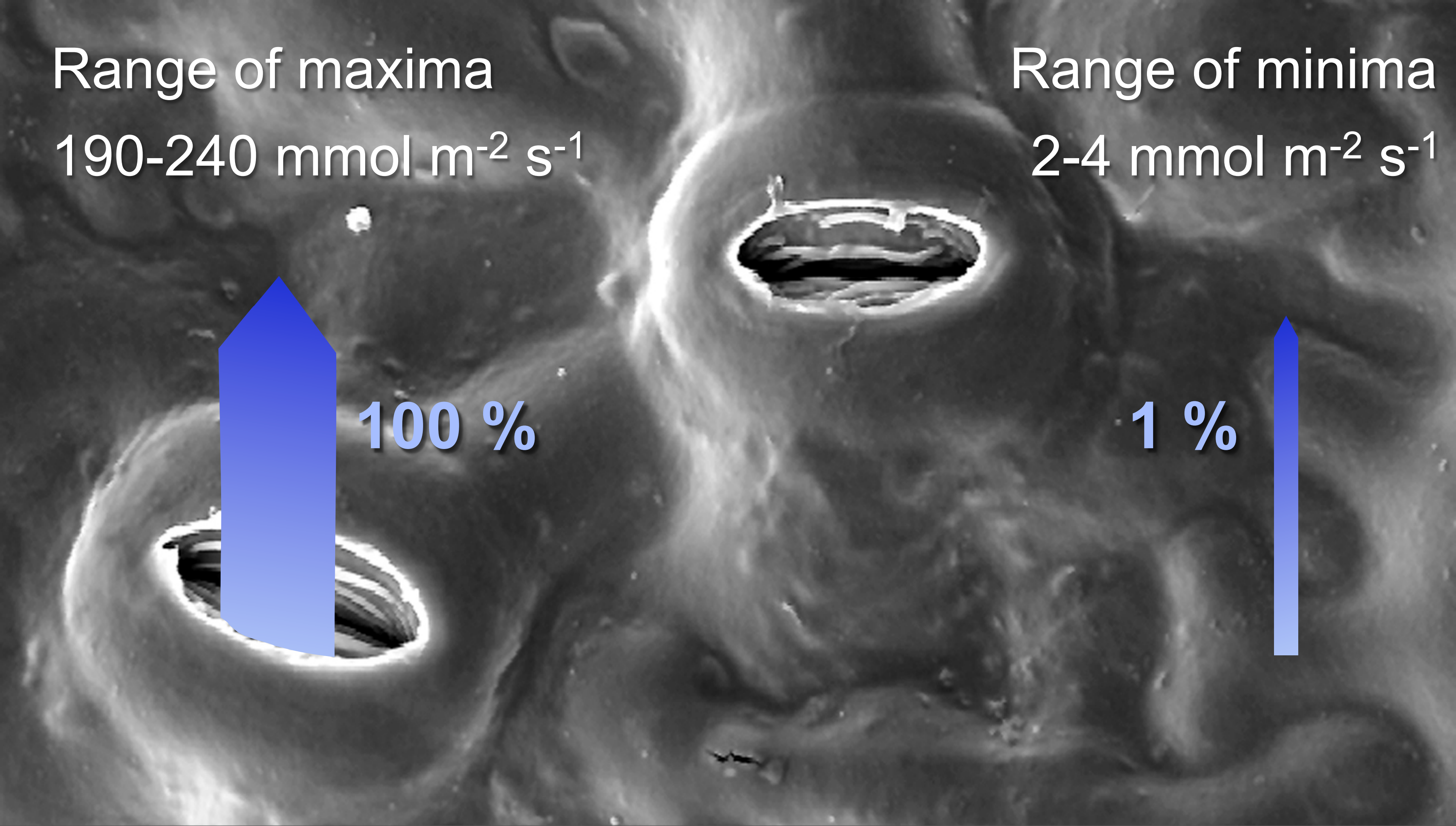
Körner C (2014) in Strasburger. Springer, Berlin

Mean <u>maximum</u> leaf diffusive conductance 218 ± 34 mmol m^{-2} s^{-1}

Mean minimum leaf conductance under desiccation

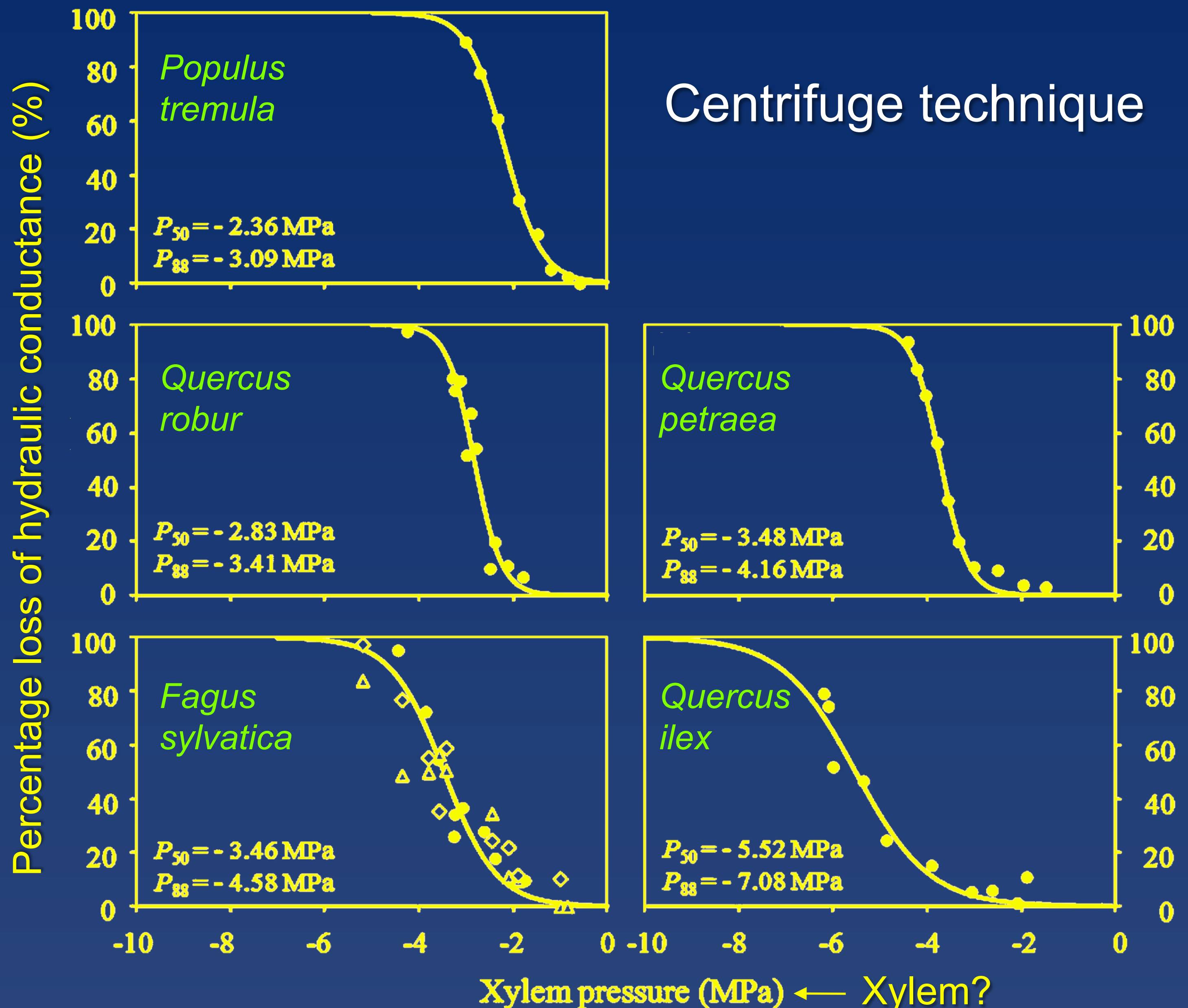
Type of vegetation	g_{min} (mmol m^{-2} s^{-1}) (n)
Boreal forest conifers	2.9 ± 0.8 (9)
Temperature deciduous forests	5.8 ± 0.8 (16)
Mediterranean vegetation	2.9 ± 0.8 (7)
Eucalyptus forests	ca. 2-5
Monsoonal forests	ca. 5
Desert shrubs(evergreen)	5.2 ± 0.9 (7)
Semi-arid subtropical/tropical shrub/tree vegetation	ca. 5
Humid tropical forests	5.0 ± 0.8 (5)

Körner C (1994) Leaf diffusive conductances in the major vegetation types of the globe. In: Schulze ED, Caldwell MM (eds) Ecophysiology of photosynthesis. Ecol Studies 100:463-490, Springer, Berlin.

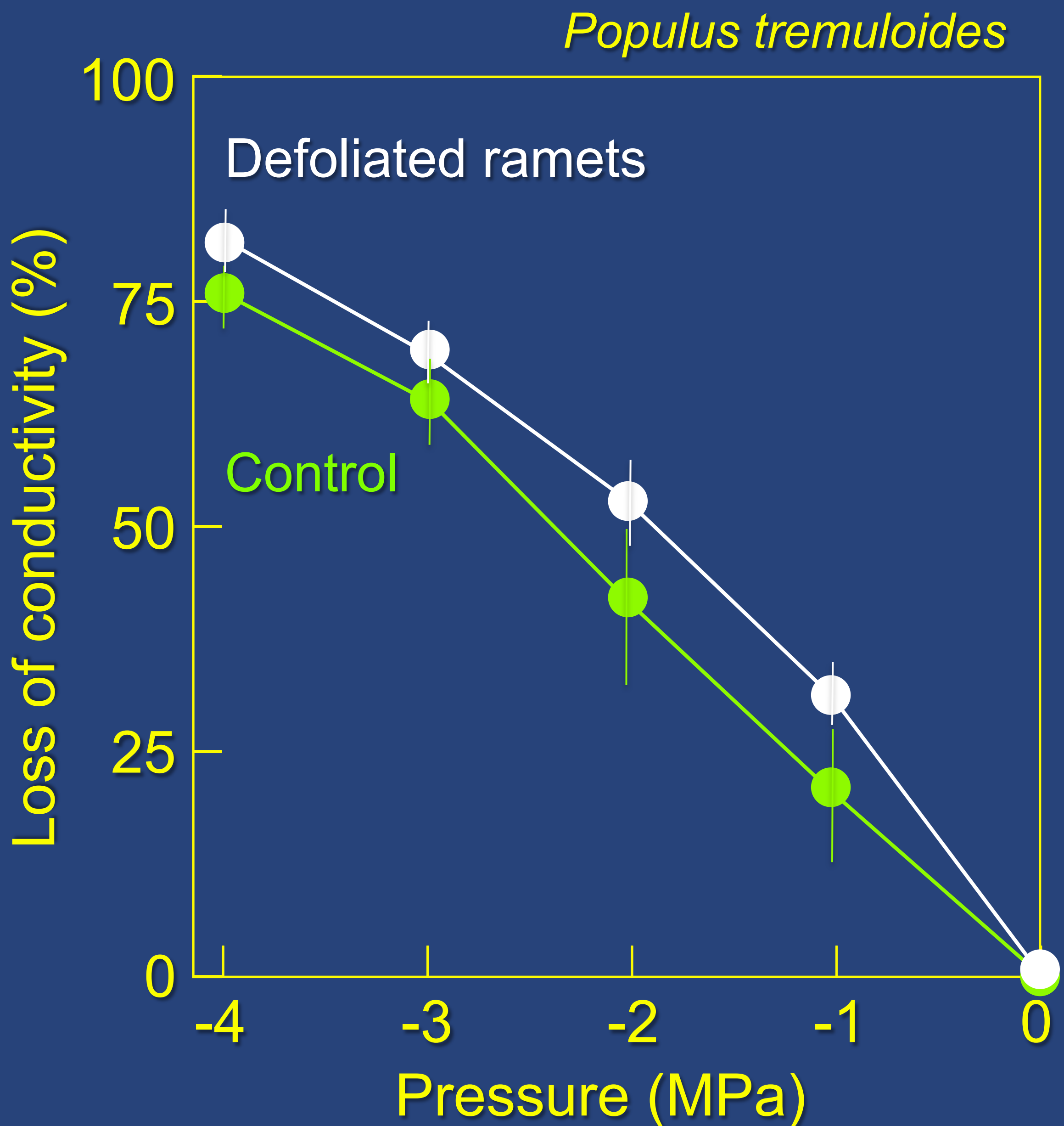


When Stomata are closed, it needs only 1 % xylem conductivity to meet demand.
Xylem- and phloem-parenchyma can cover cuticular transpiration for several month without water uptake by roots.

Centrifuge technique



Urli M *et al* (2013) Tree Physiol 33:672-683



Anderegg WRL & Callaway (2012) Plant Physiol 159: 1866

Can phloem transport limit sink activity (e.g. tissue growth)? → unlikely

"The transport pathway does not normally exert any control over sink growth and cereal roots do function near to saturation"

Review by Minchin PEH *et al* (1993) J Exp Bot 44:947

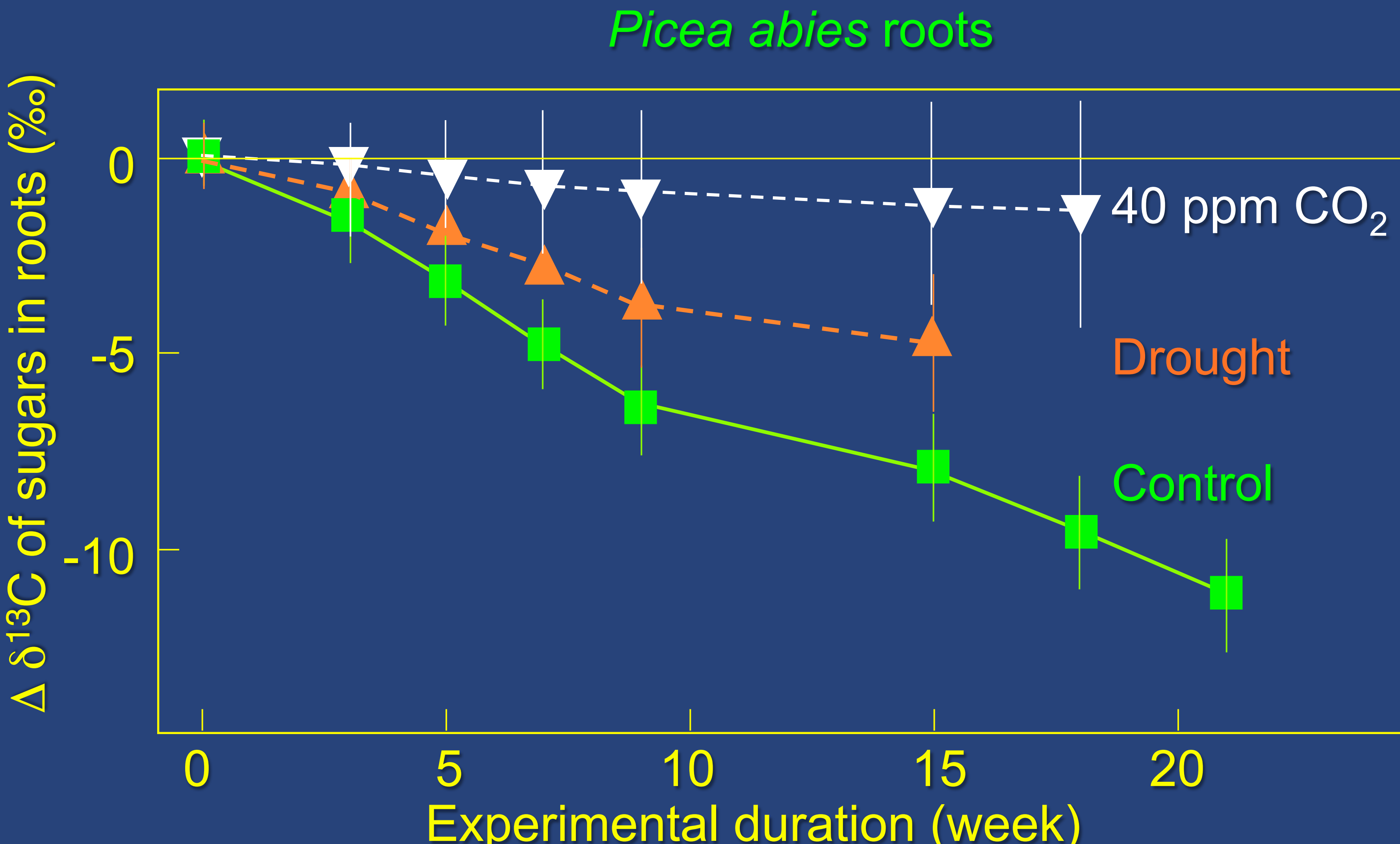
→ Thus, sink limitation is a property of the sink (restriction of tissue growth)

Carbon reserves are allocated even under extreme drought (^{13}C tracer signals)

Hartmann H *et al* (2015) Tree Physiol 35:243

→ Thus, there is phloem transport

$\delta^{13}C$ data show that C is allocated to below-ground storage pools even under severe C limitation



Hartmann H *et al* (2015) Tree Physiol 35:243-252

Summer drought in grassland

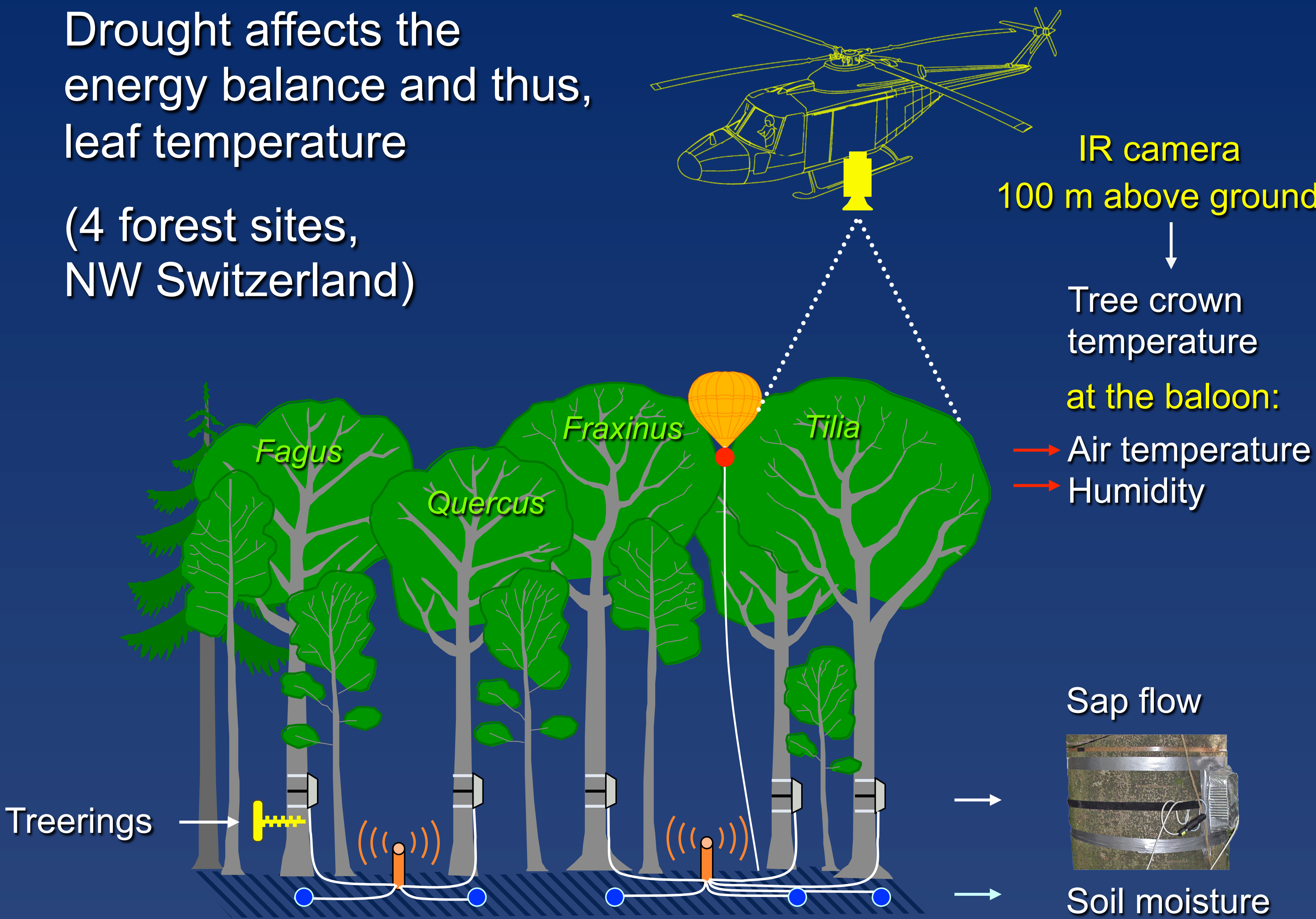
Severe soil moisture deficit decreased the ecosystem C uptake and the amounts and velocity of C allocated from shoots to roots.

However, the proportion of recently assimilated C translocated belowground remained unaffected by drought.

Hasibeder R *et al* (2015) New Phytol 205:1117

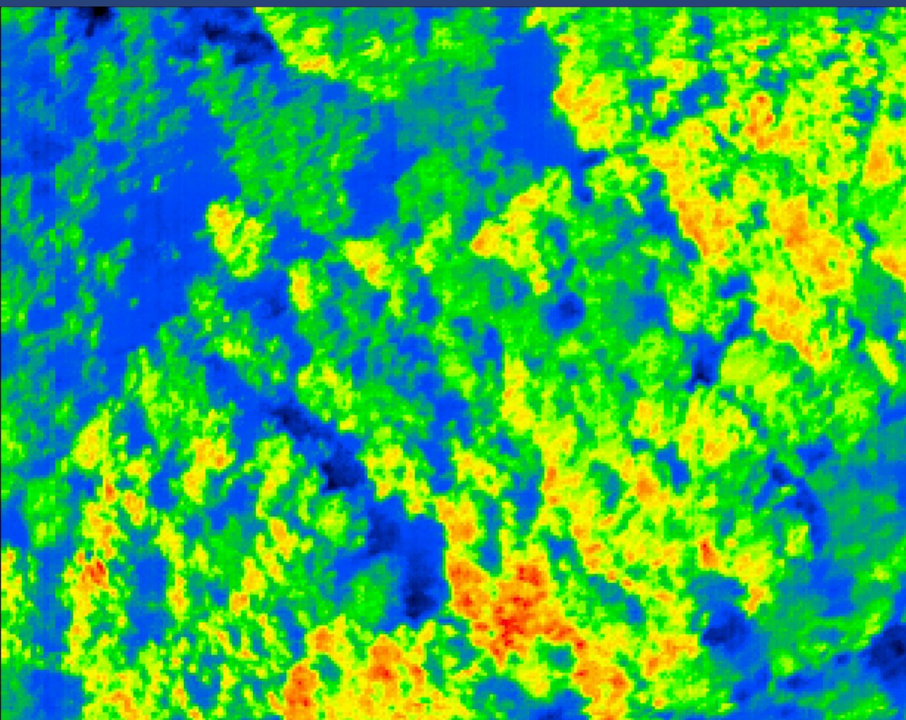
Drought affects the energy balance and thus, leaf temperature

(4 forest sites, NW Switzerland)

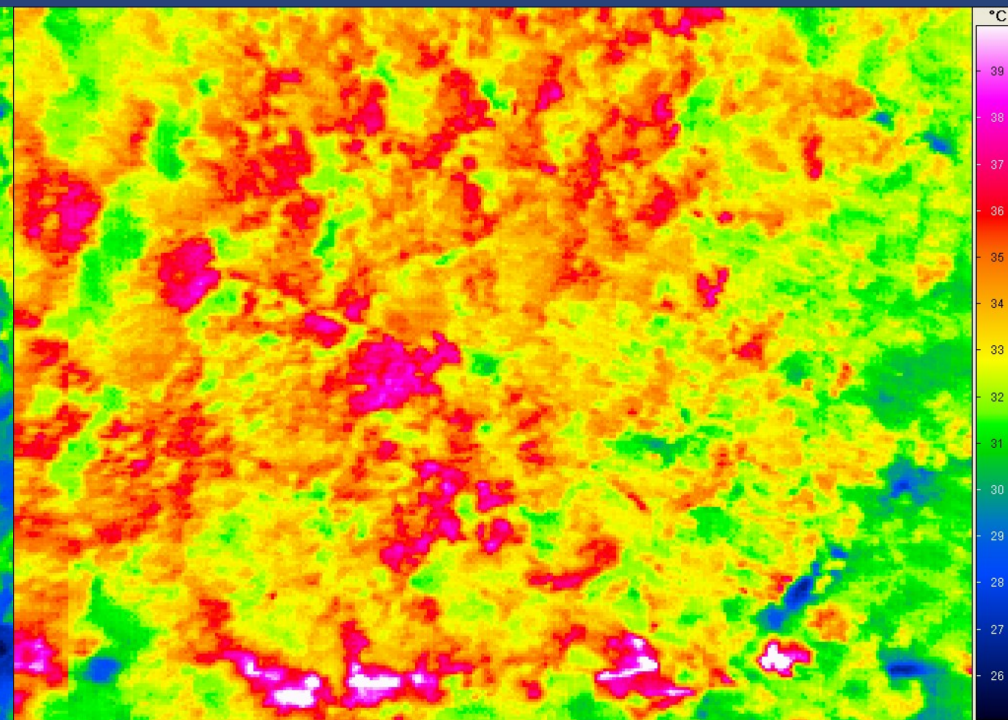


Thermal images after 4 weeks of drought

Wet site



Dry site



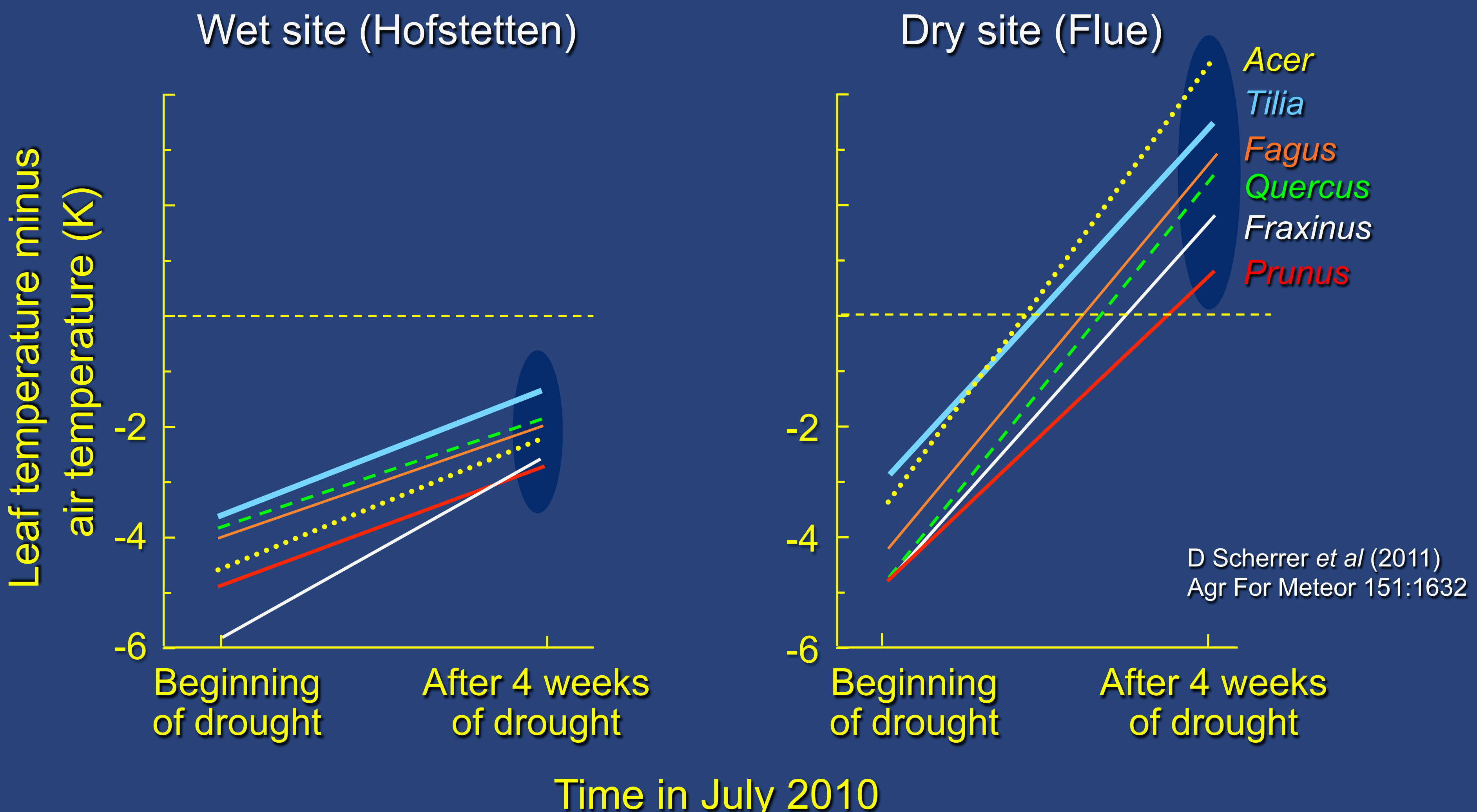
Date: 16-07-2010
Time: 15:30
Mean tree crown temperature: 30.6 °C

Date: 16-07-2010
Time: 15:31
Mean tree crown temperature: 33.9 °C

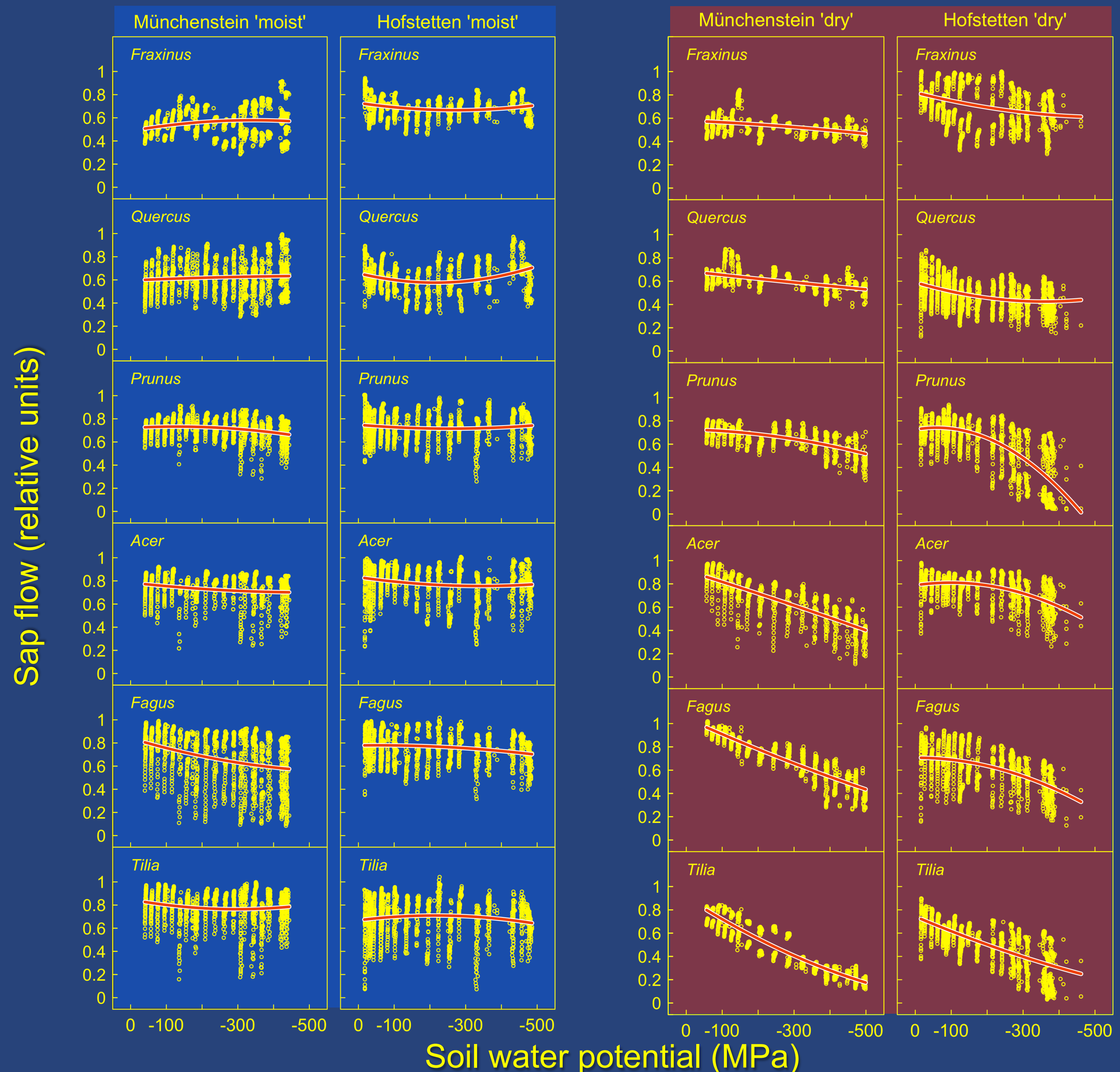
D Scherrer *et al* (2011) Agr For Meteor 151:1632

Difference between tree crown surface temperature (IR) and air temperature (baloon) for a dry and a wet site during a period of increasing drought.

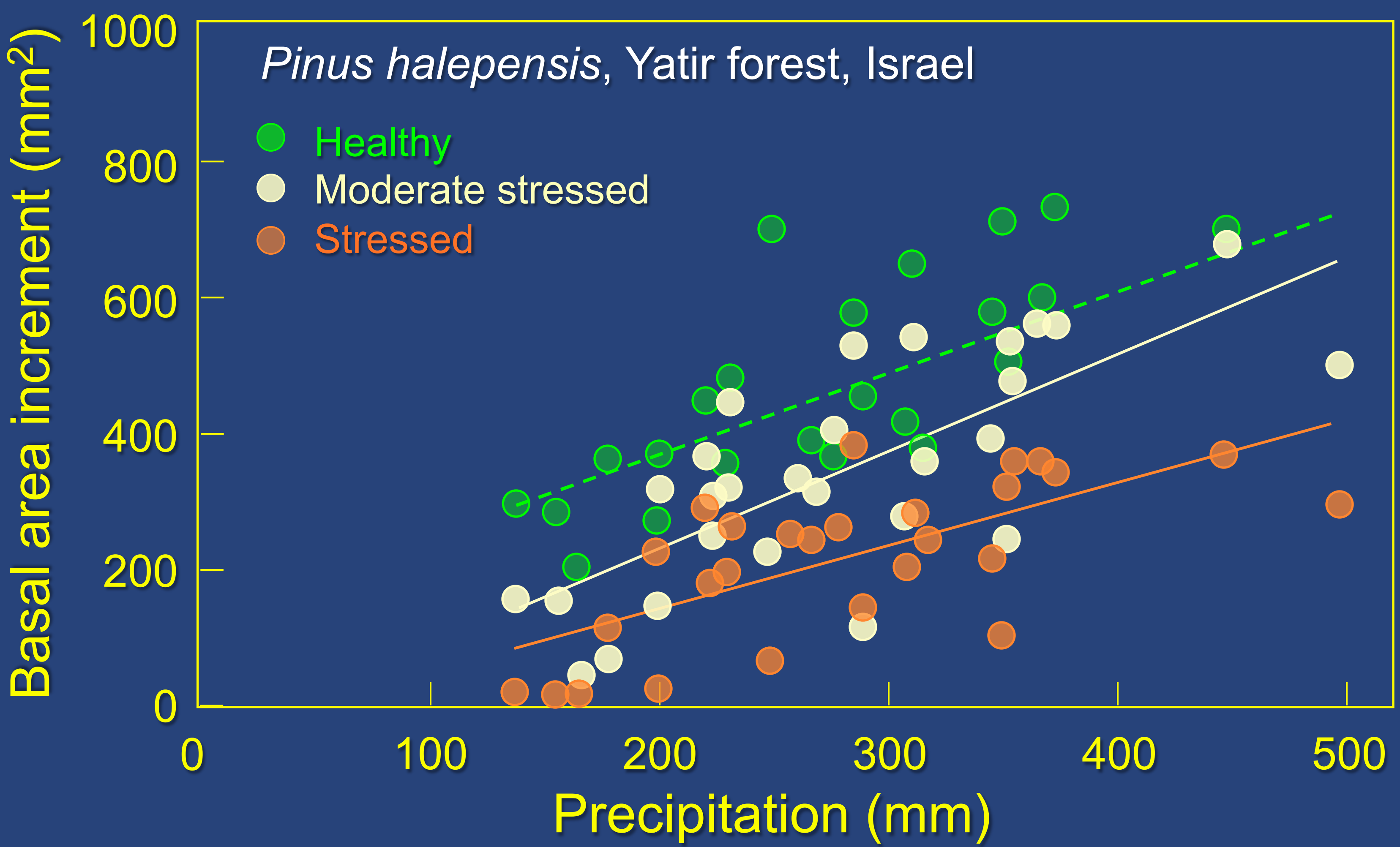
The ranking of tree species remains largely conserved.
Tilia is always warmest and *Acer* most sensitive.



Sap flow during drought



There is a predisposal of mortality



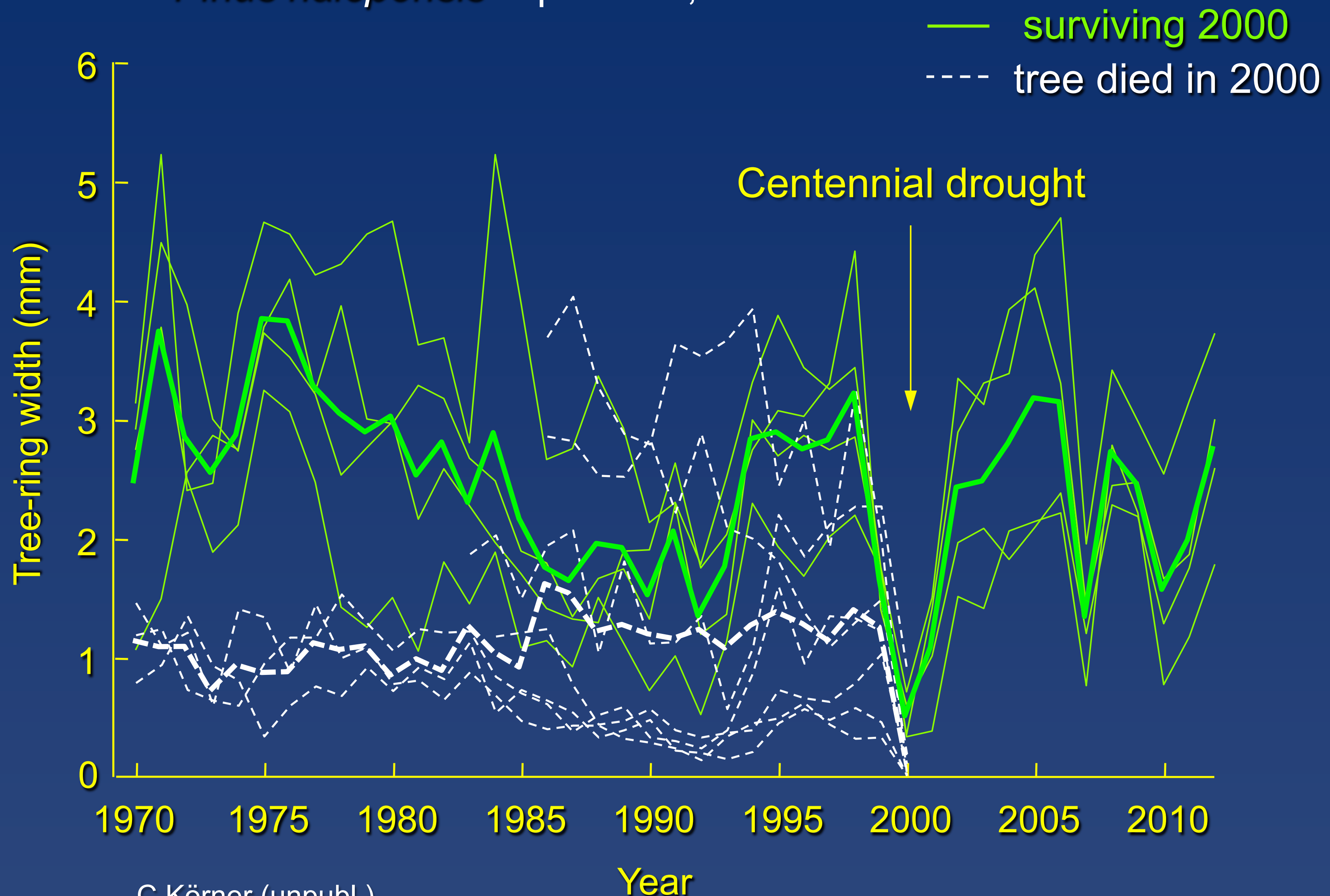
Klein T *et al* (2014) Tree Physiol 34:981


When it gets really dry ...
Is the Sahara moving north?
(Samos, Greece,
centennial drought 2000)


50 years old trees died

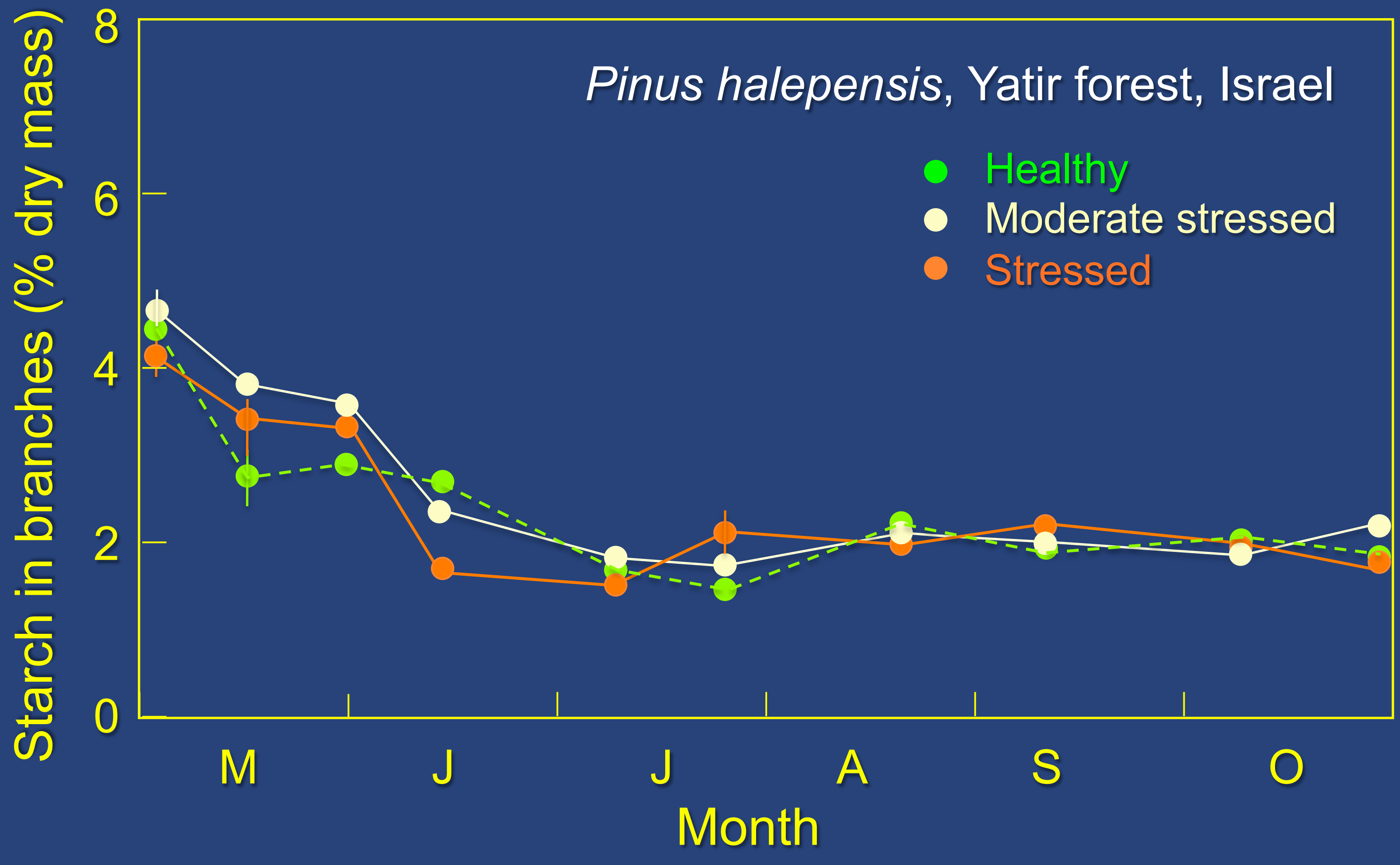
Tree growth (ring width)

Pinus halepensis ssp. *brutia*, Samos



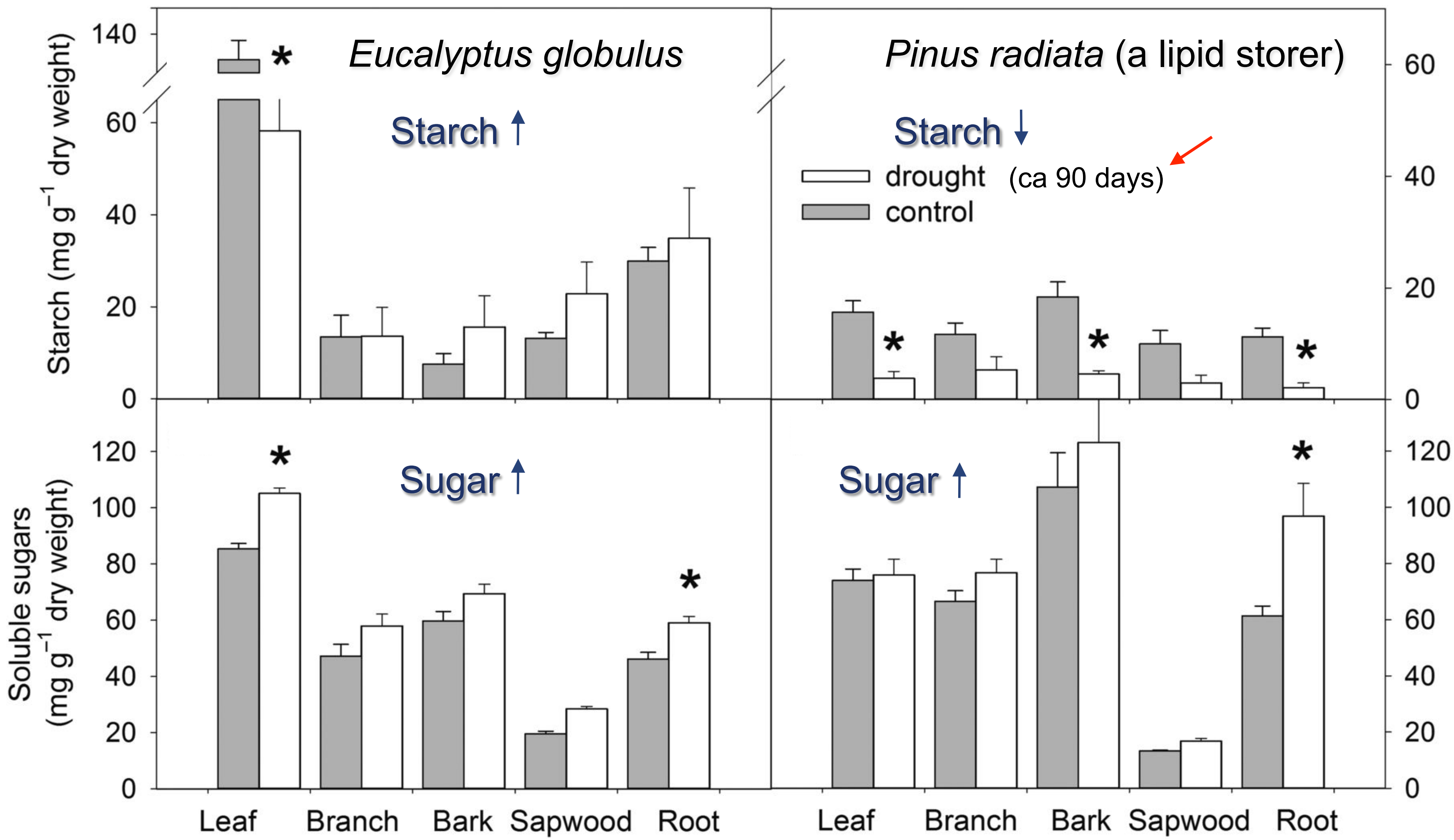
C Körner (unpubl.)

What happens to storage reserves during drought



Klein T *et al* (2014) Tree Physiol 34:981

Organs, type of reserve and species matter for reserves under drought



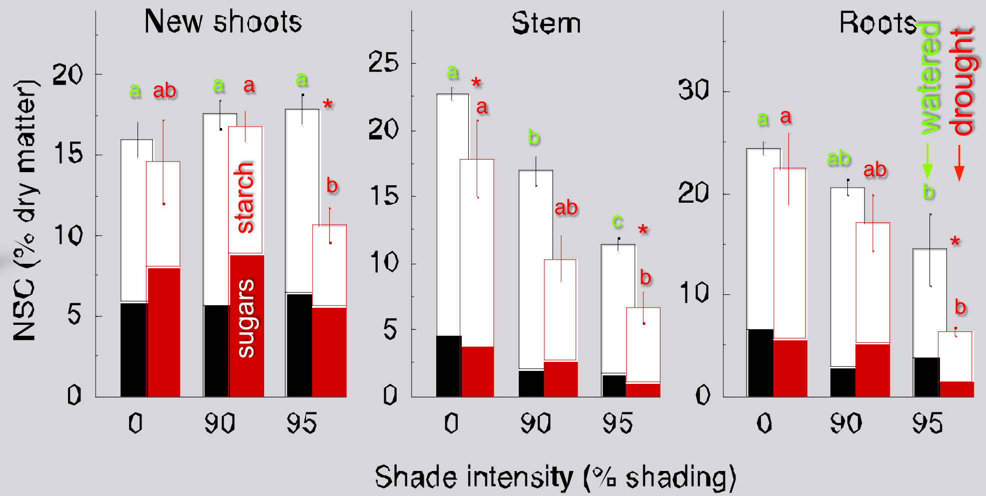
... but no evidence that reserve pools are ever depleted in these potted saplings

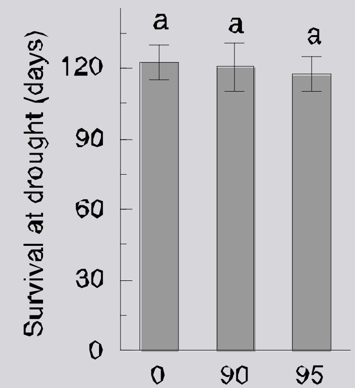
Mitchell P *et al* (2014) Tree Physiol 34:443-458

NSC during severe drought x light

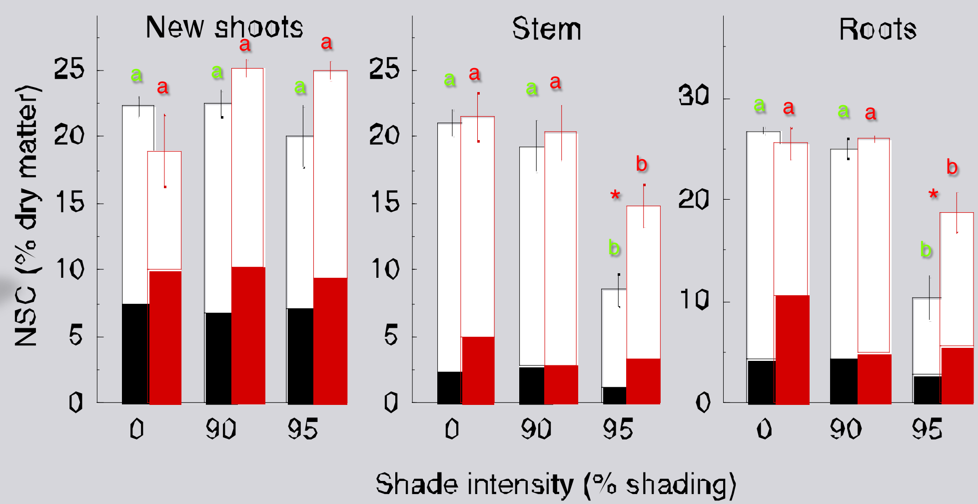
Drought survival of potted saplings 4 month

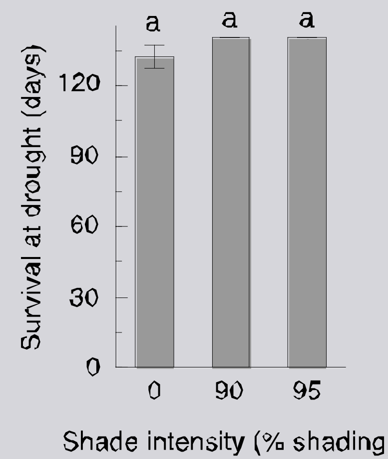
Carpinus betulus





Quercus petraea

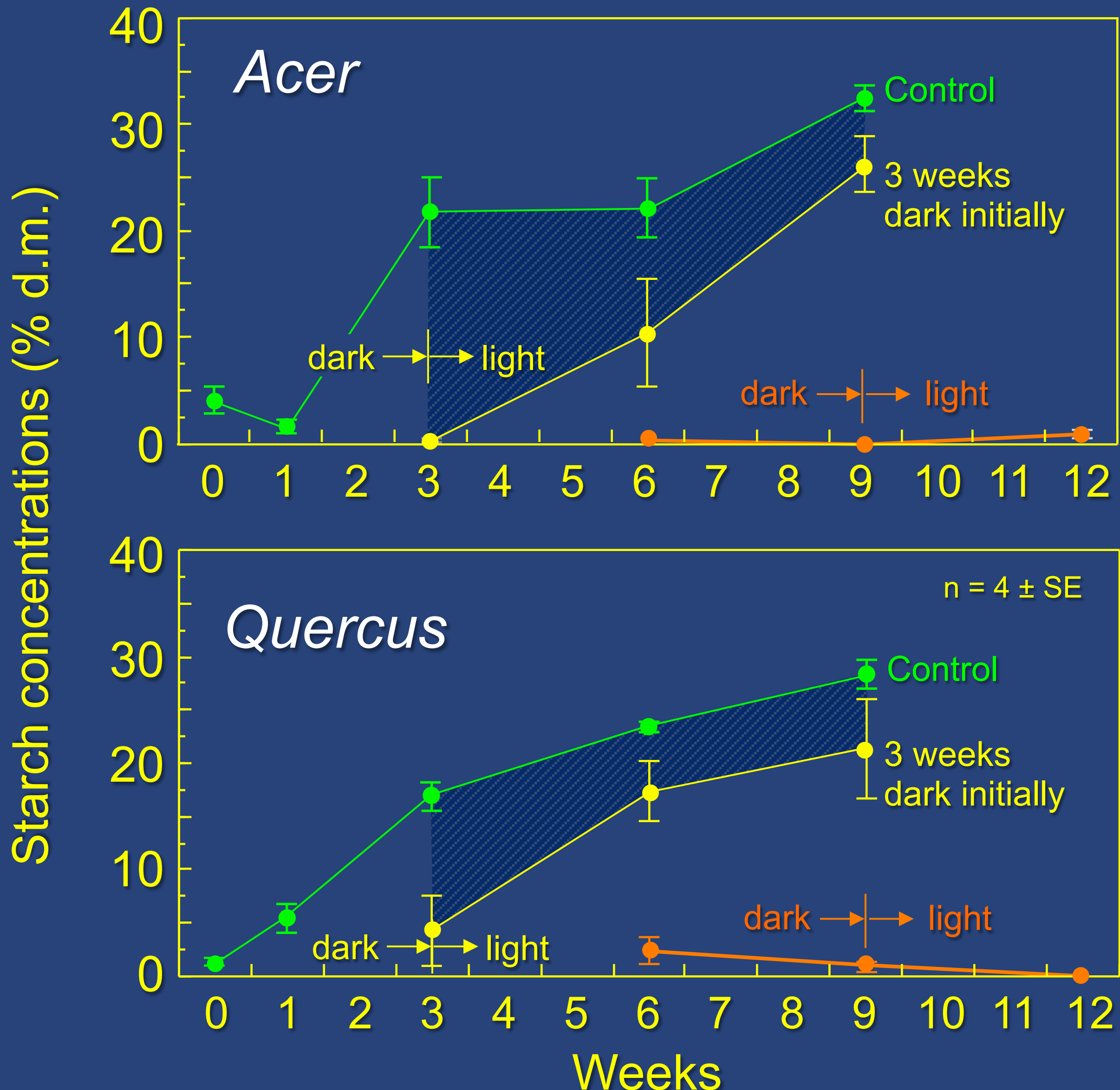




* Significant difference between drought and control at $p < 0.05$

A. Mösch & G Hoch (Basel), unpubl.

Stem sapwood

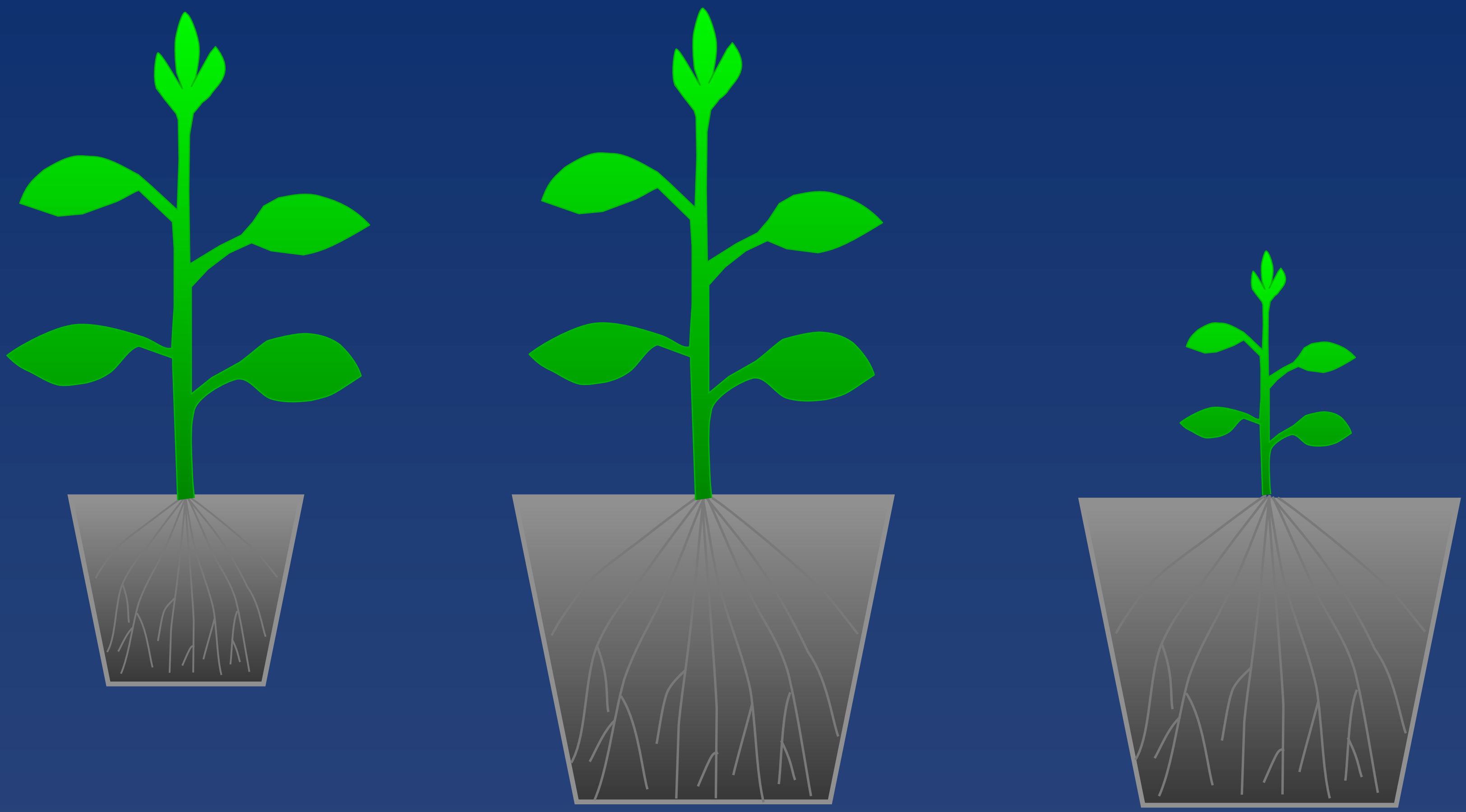


A. Schwendener & G. Hoch (Basel), unpubl.

Methods I

Desiccation experiments in containers are prone to bias.

Assume the same treatment is applied to



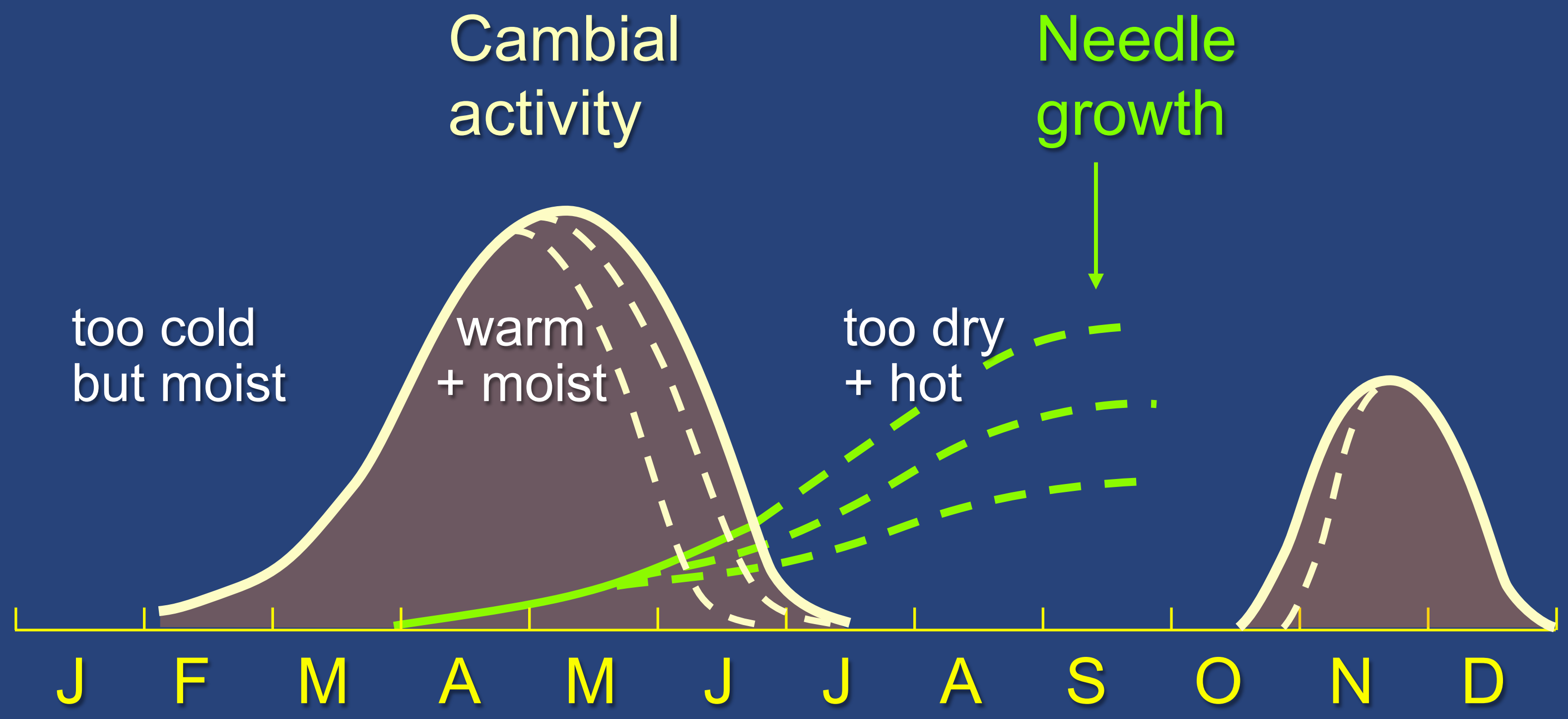
The plant size - pot volume ratio matters.

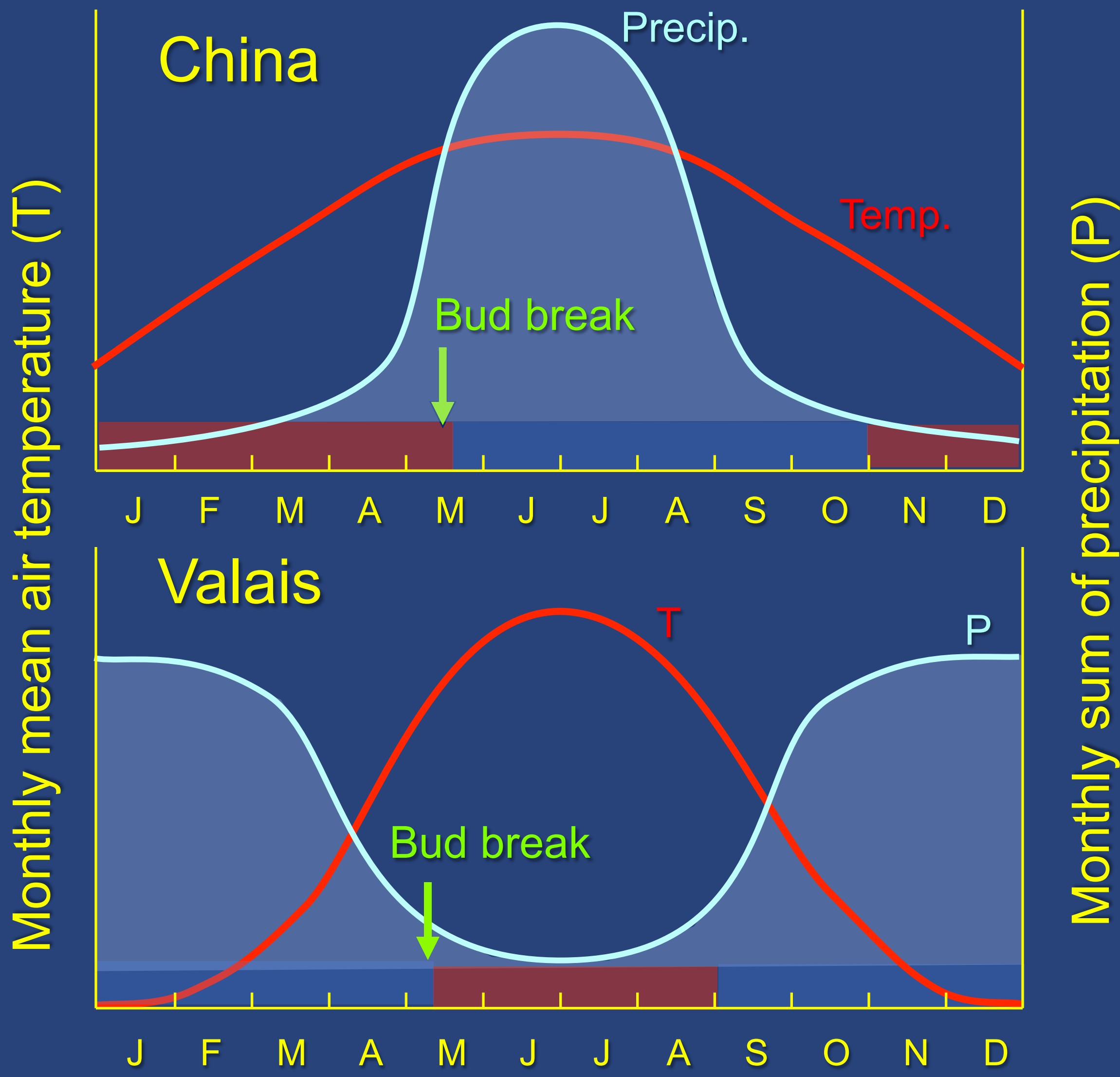
Methods II

Pine phenology in the Mediterranean

Looking for isotope and growth signals, timing of tissue formation and stress is key.

→ No isotope signals during periods when no tissue is formed.





From dry to wet:

→ Survival of long drought during quasi dormant state

From wet to dry:

→ Growth coincides with water shortage

F Baumgarten, G Hoch, C Körner (Basel) unpubl.

Benzilan, N-Yunnan, the lower treeline (dry interior valley) at ca 2700 m a.s.l.

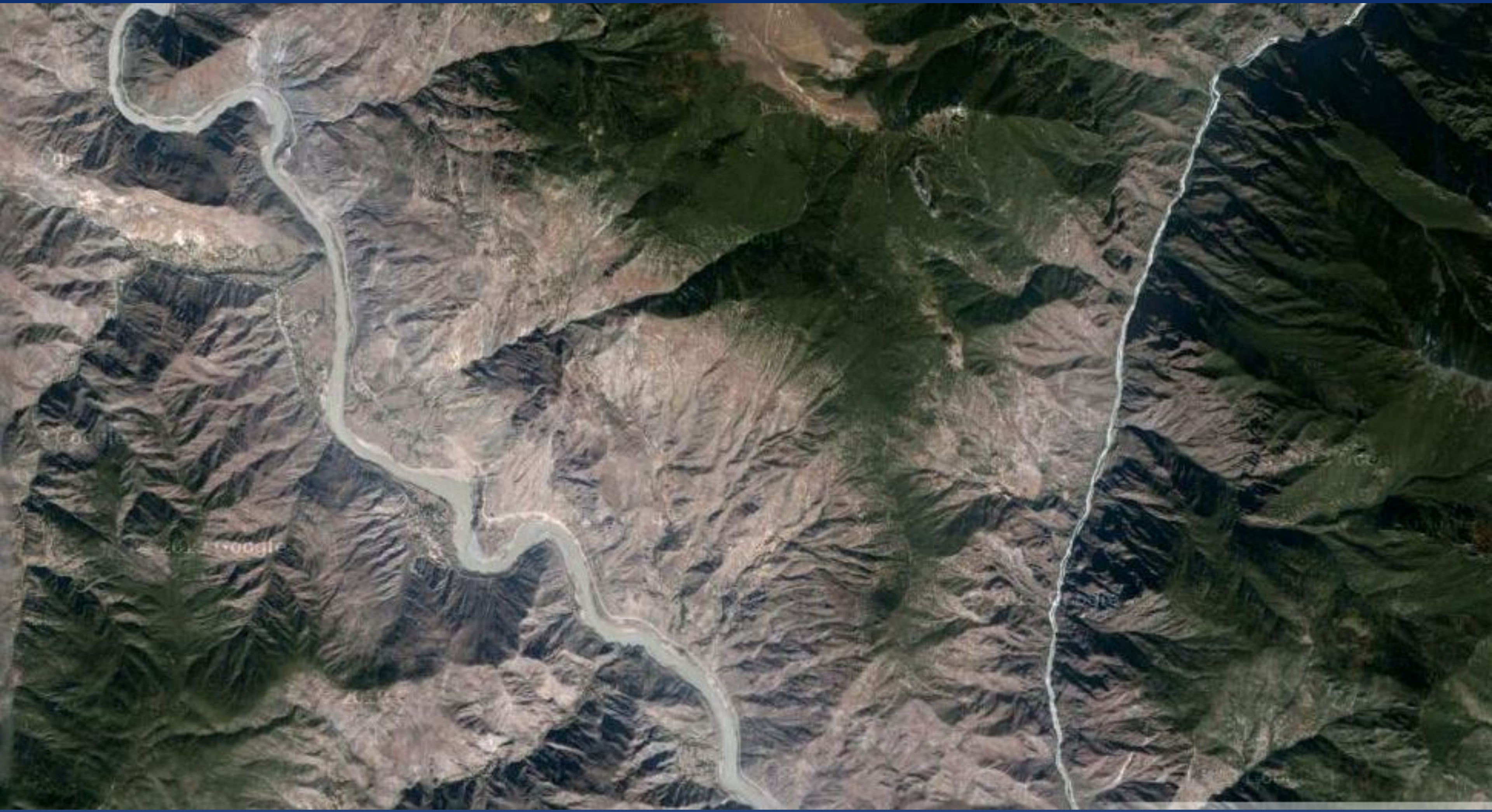


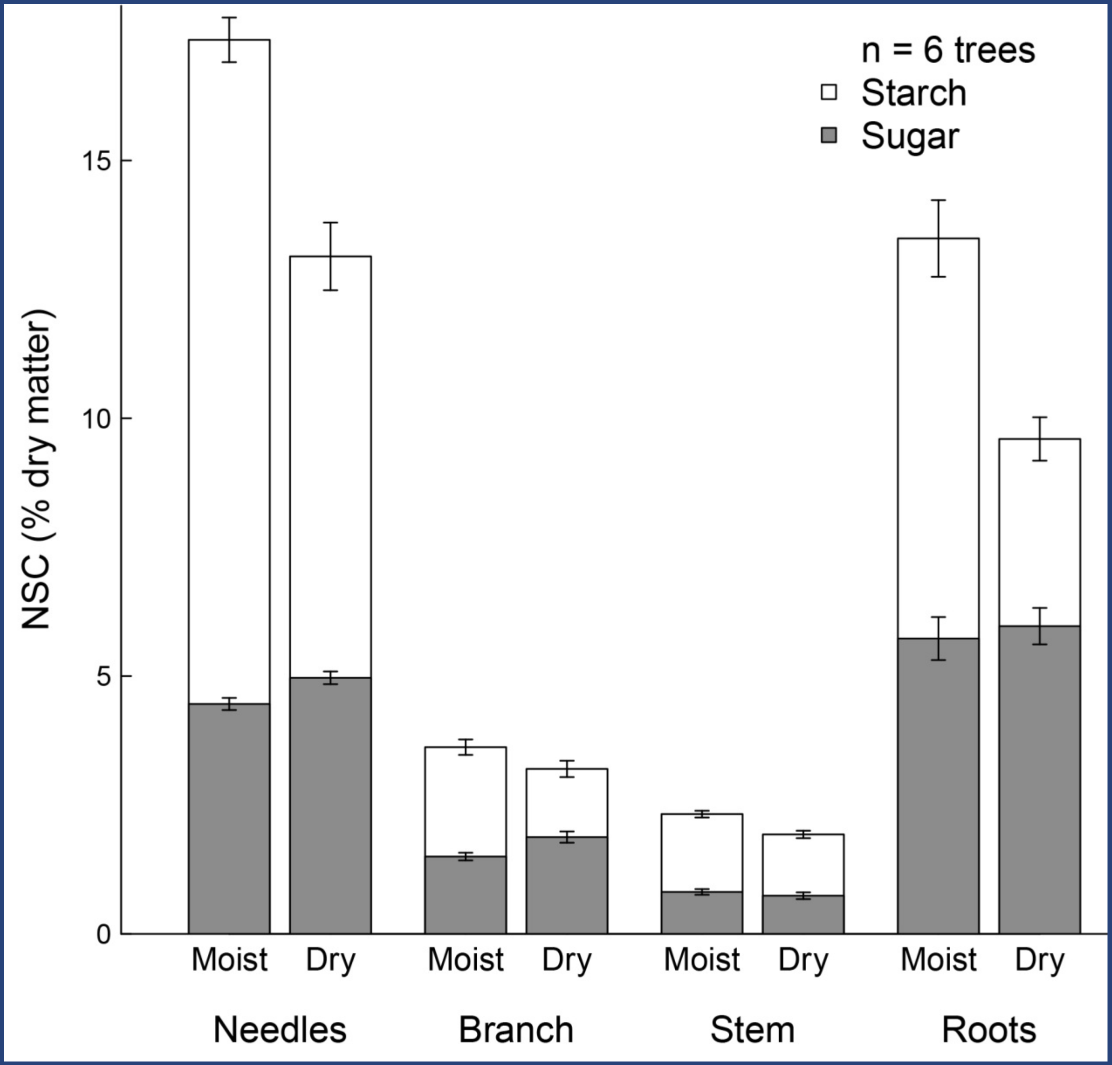
photo: F. Baumgarten

Benzilan, N-Yunnan, the lower treeline (drought)

All land area that receives more than 250 mm of rainfall per year and has a seasonal temperature above 6.4 °C is able to support tree growth.

At the dry edge, minute changes in the monsoon regime have dramatic effects on tree growth.

NSC Yunnan



At the end of the 7-8 month dry season (May)

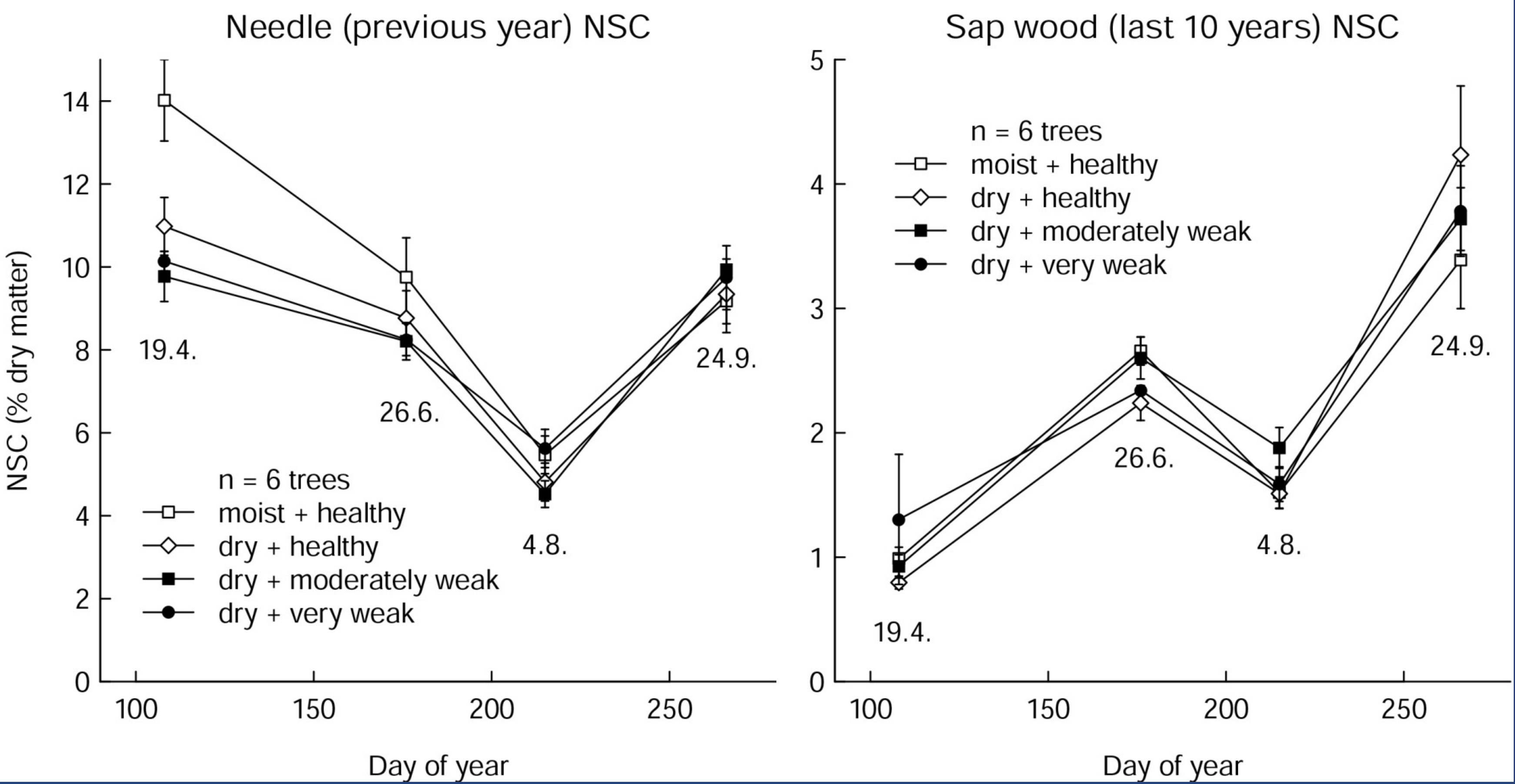
→ no change in sugar

→ mild reductions in needles and roots

F Baumgarten, G Hoch, C Körner (Basel) unpubl.

NSC Valais x degree of crown decline

→ no effect on NSC



F Baumgarten, G Hoch, C Körner (Basel) unpubl.

- There is no hint of carbon starvation at both sites (China and Switzerland)
- China: survival of drought during the dormant (winter) period, moist conditions during the monsoon (high basal area increments)
- Switzerland: moist winter conditions, growth restriction during dry summer period (low basal area increments)

Conclusion:

when trees die under drought

→ 'Classical' tissue desiccation damage with or without xylem conduit failure is most likely.

→ Carbon starvation is quite unlikely/rare, and ... needs high time resolution data when experimentally induced.

- The biosphere is currently not carbon limited
- Carbon is unlikely critical for mortality under drought
- It is the entire hydraulic system and desiccation tolerance which matter

In a double sense: ... back to the roots

‘Classical‘ water relations science

Rooting depth is key