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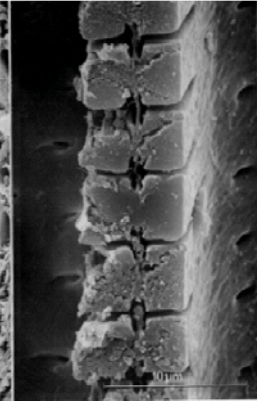
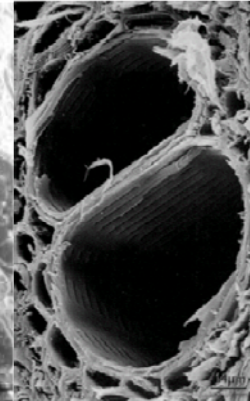
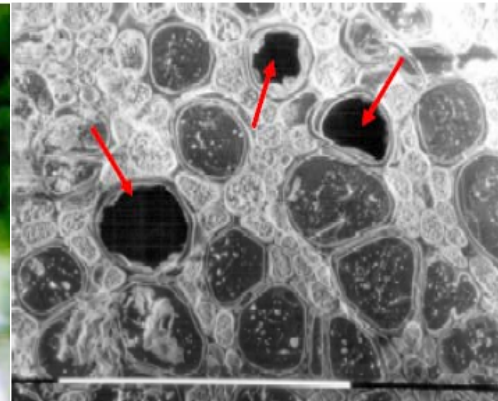
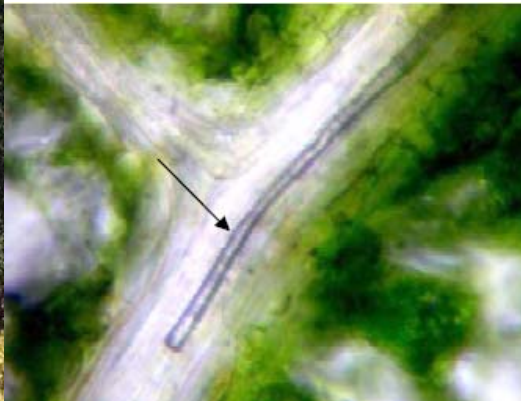


Biodiversité, gènes & communautés



Institut National de la Recherche Agronomique

Stress and adaptation to stress



Définitions

Stress: est considéré comme étant une déviation significative des conditions optimales de vie – c'est une contrainte externe qui empêche le fonctionnement normal d'un système.

Strain: la déformation induite par le stress dans le système.

Régime de stress: fréquence, périodicité, intensité, durée.

Définitions

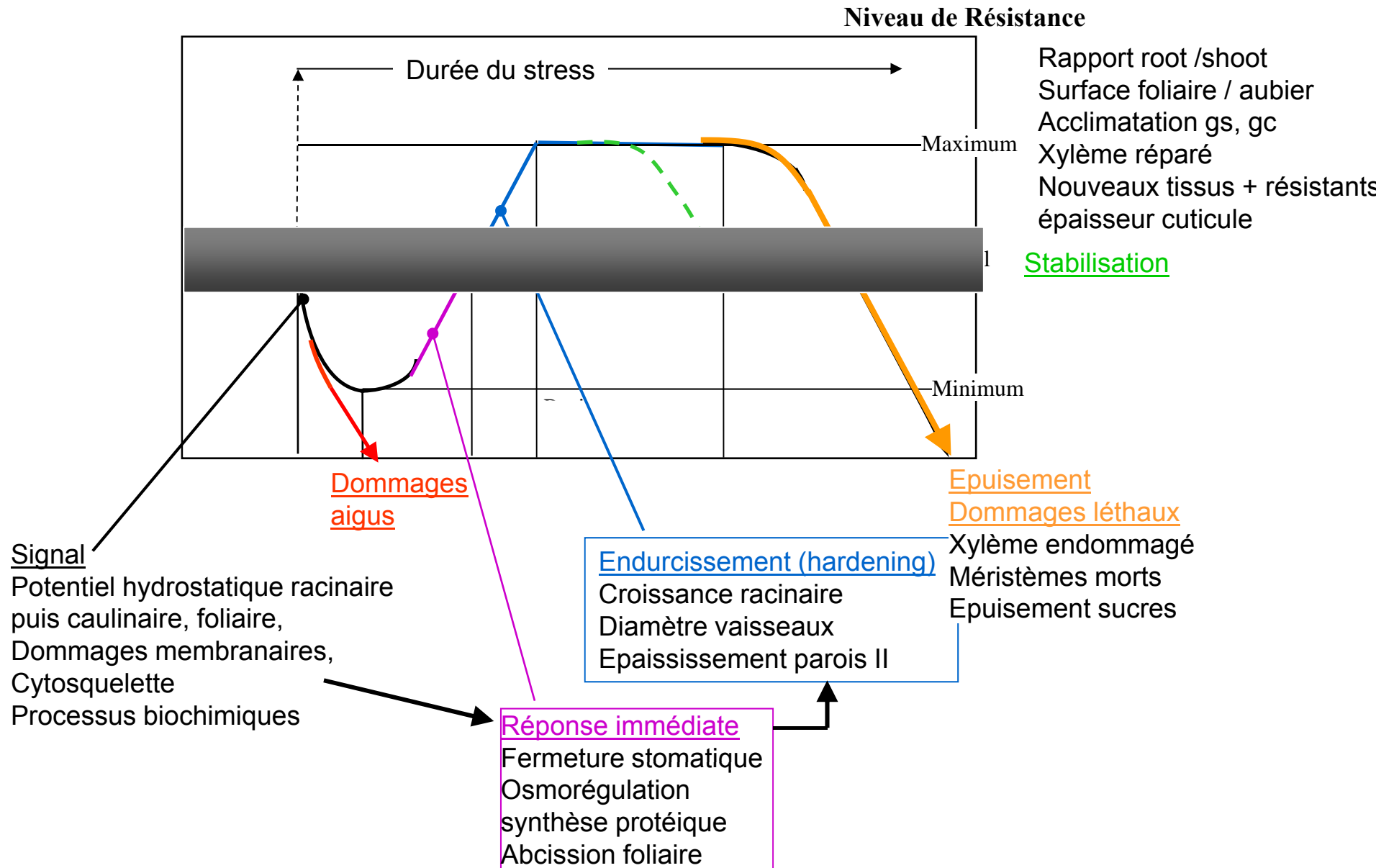
Acclimation: if tolerance increases as a result of exposure to prior stress, the plant is said to be acclimated or hardened.

Acclimation can be distinguished from adaptation

Adaptation: usually refers to genetically determined level of resistance acquired by a process of selection over many generations.

To add to the complexity, gene expression plays an important role in acclimation.

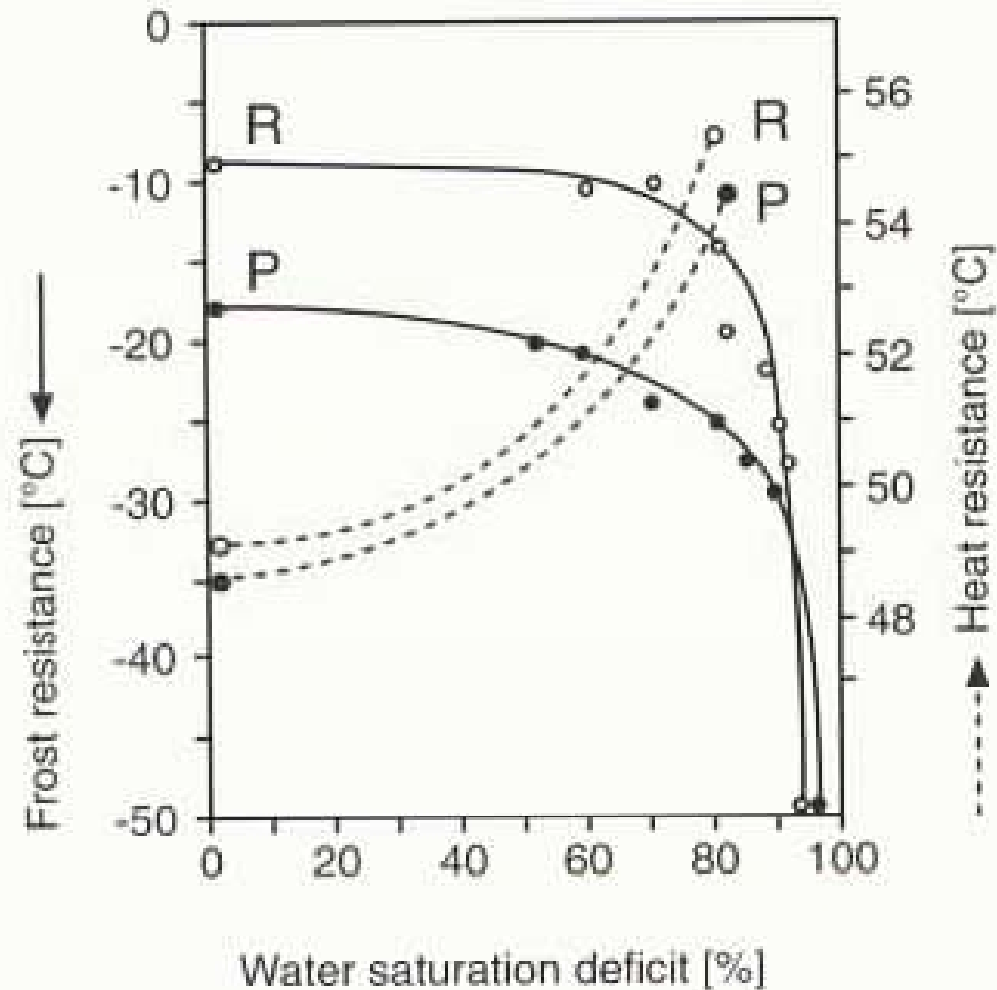
La réponse au stress : réponses immédiate, différée, endurcissement, acclimatation et rupture.



La réponse au stress : traits généraux

Threshold temperatures of resistance to heat and to frost

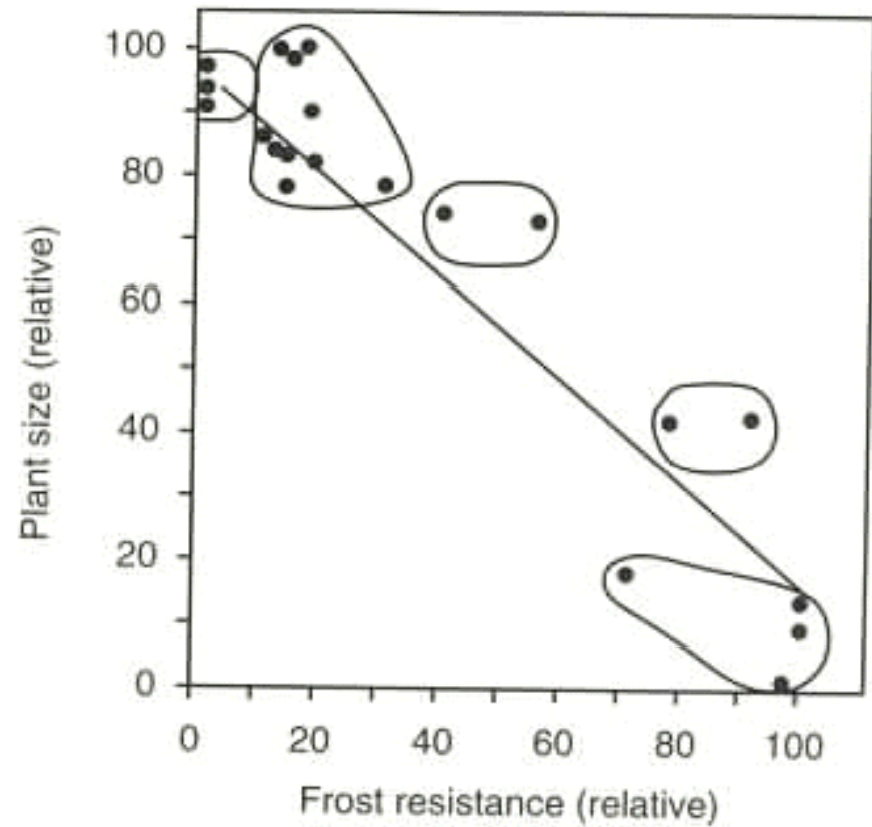
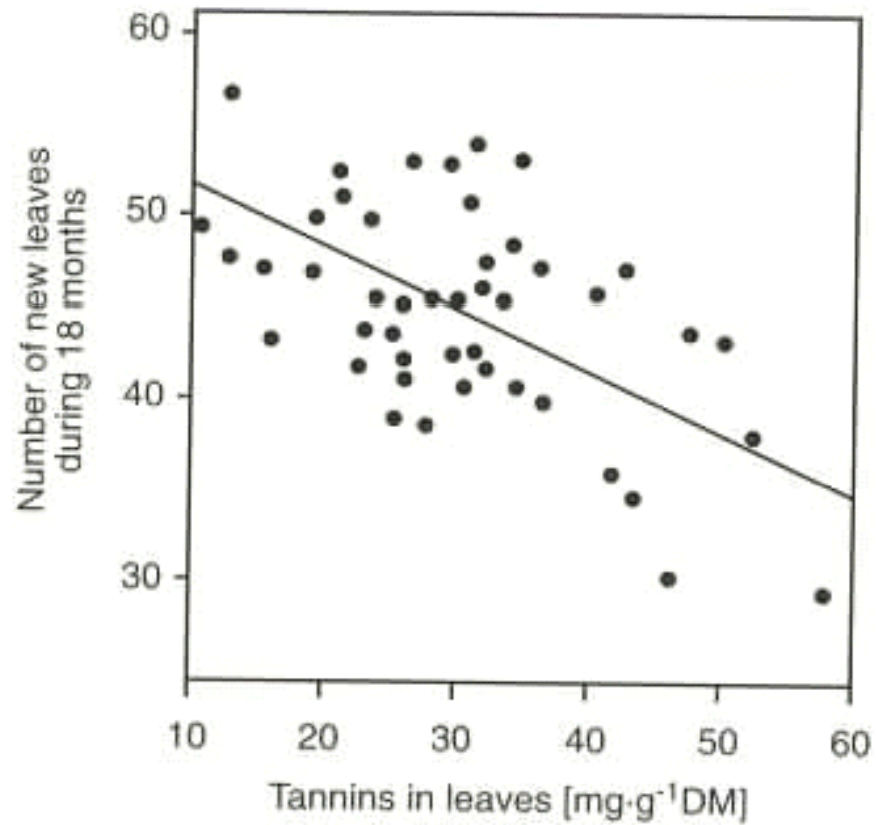
- Acquisition de résistances
- Les plantes répondent souvent à une combinaison ou à une série de stress



Mechanisms associated with the coupled acquisition of two forms of resistance are stress induced proteins that stabilize the structure of the protoplasm.

La réponse au stress : traits généraux

- Coût de la mise en place d'une résistance au stress



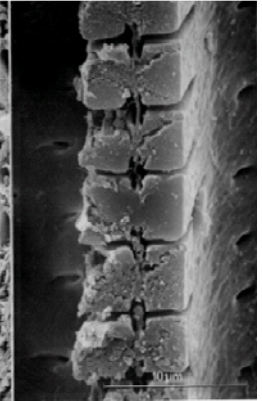
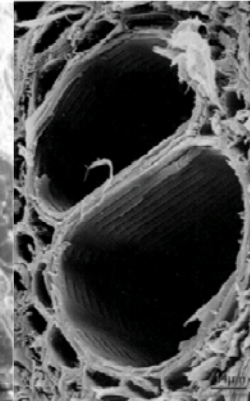
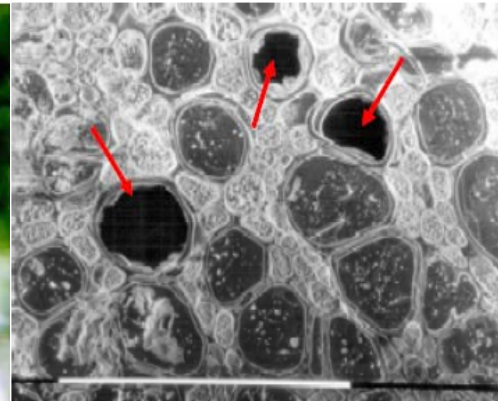
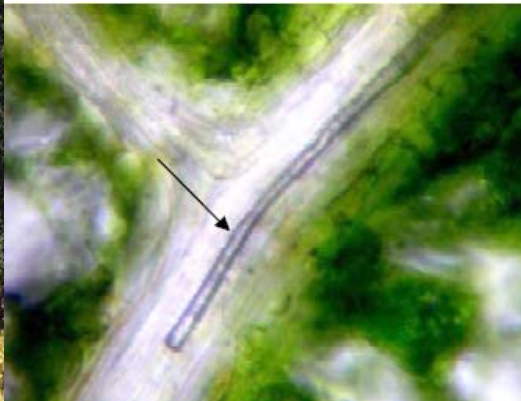
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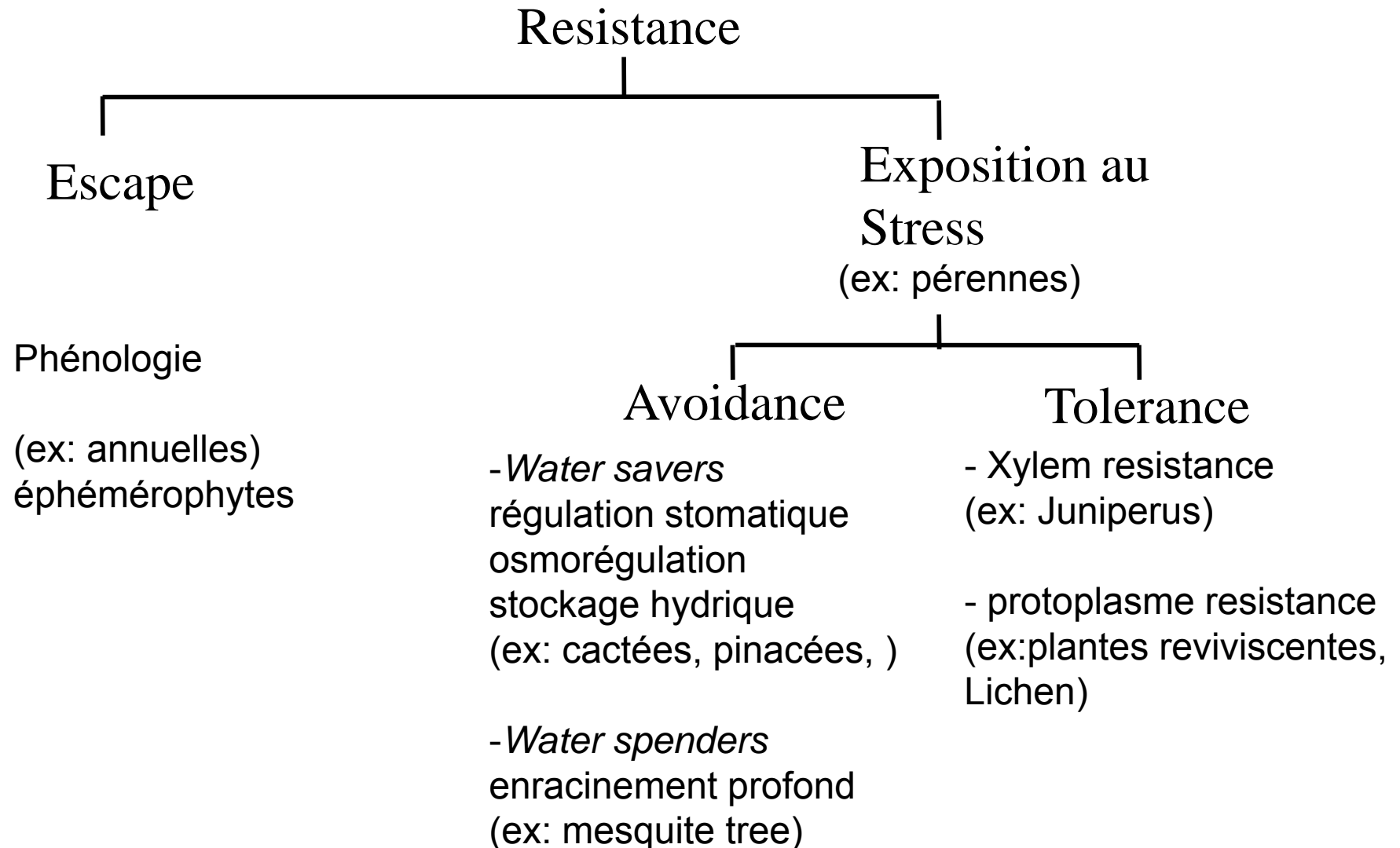
Story I. Drought and strategies



Réponse au stress hydrique : traits généraux

- Ajustement osmotique cellulaire : maintien de l'équilibre hydrique (turgescence) par augmentation de la concentration en ions
- réduction de la surface foliaire (via une diminution de la turgescence et un arrêt de croissance ou une chute de feuille lié à une cavitation au niveau du pétiole)
- Biosynthèse de protéines de stress et métabolites secondaires (coût en énergie élevé)
- Hormones de stress: ABA, Ethylène → réponse intégrée de la plante entière
- Fermeture stomatique (hydropassive et hydroactive), baisse de photosynthèse et production, respiration accrue
- Allocation du carbone : compromis entre croissance en dimension *versus* résistance aux stress.

2. Les types de réponse à la contrainte hydrique: plusieurs manières de résister à la sécheresse



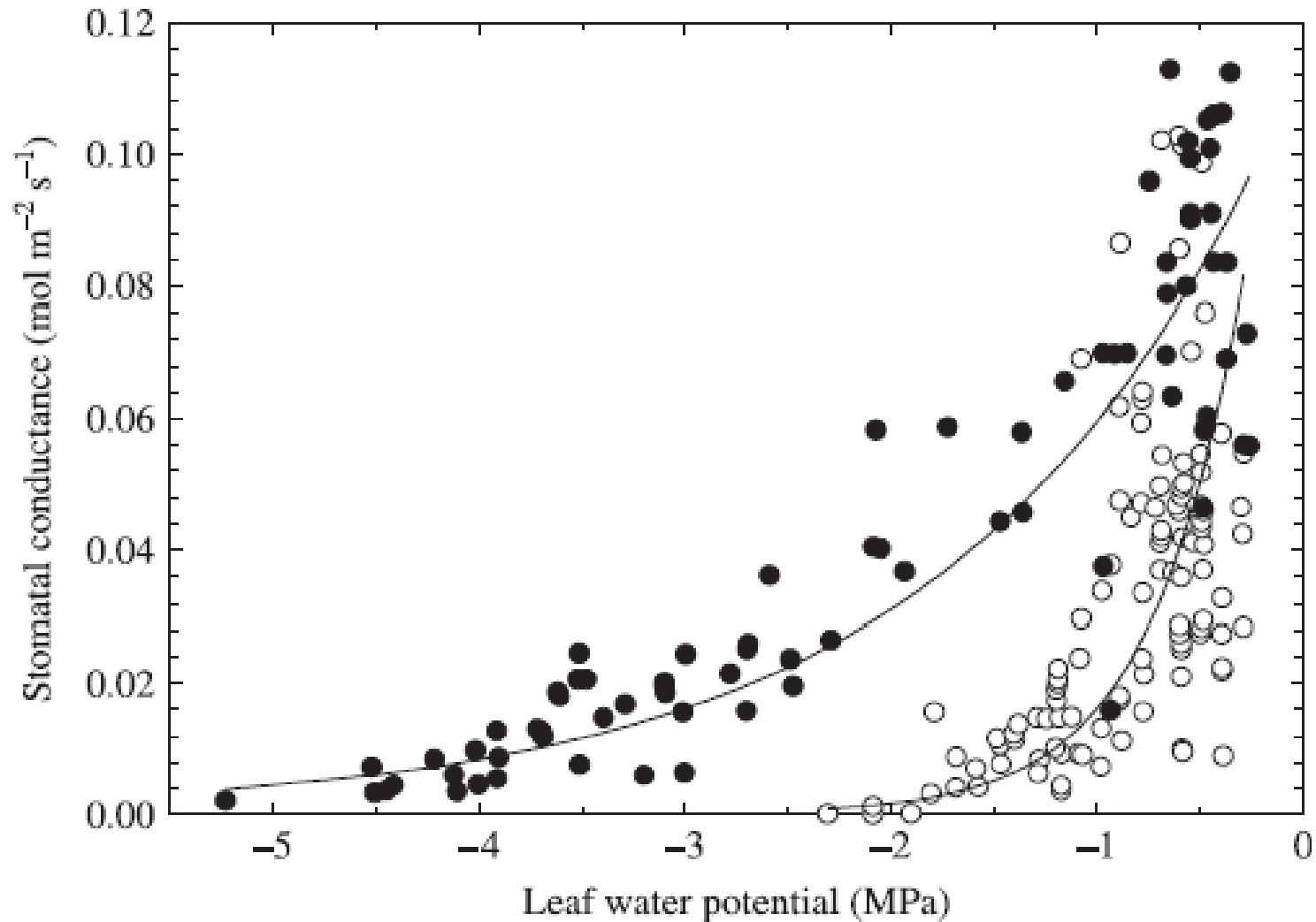
2. Les types de réponse à la contrainte hydrique: plusieurs manières de résister à la sécheresse

Drought escape: escape strategy consists in adjusting leaf phenology to minimize coincidence of sensitive growth stages with expected periods of drought.

Desiccation postponement: avoidance strategy consists in reducing losses during periods of stress, closing stomata or allocating carbon for deeper roots. (the ability to maintain tissue hydration)

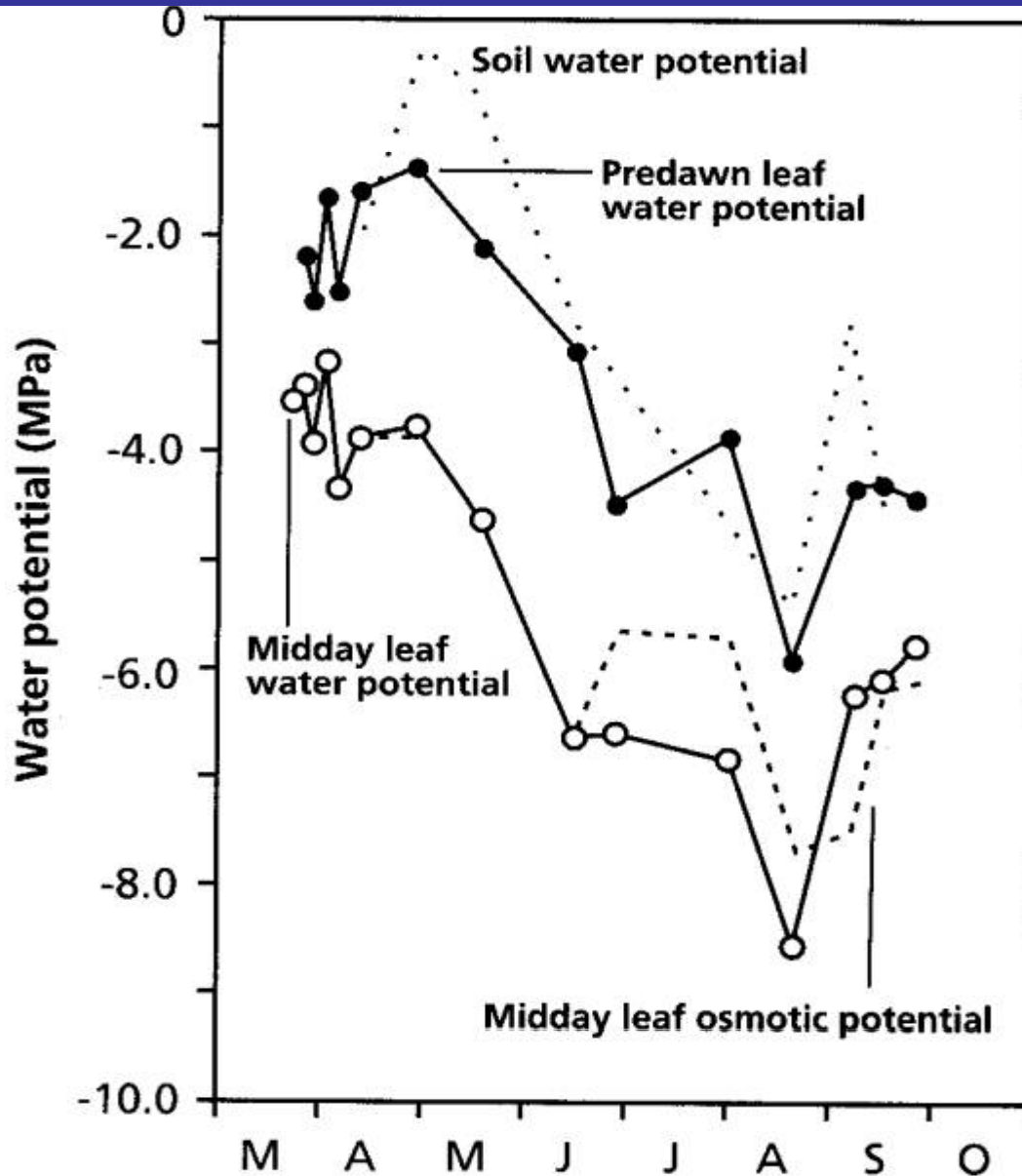
Desiccation tolerance: tolerance strategy consists in withstanding drought by increasing xylem resistance to cavitation.

2. Isohydry and anisohydry



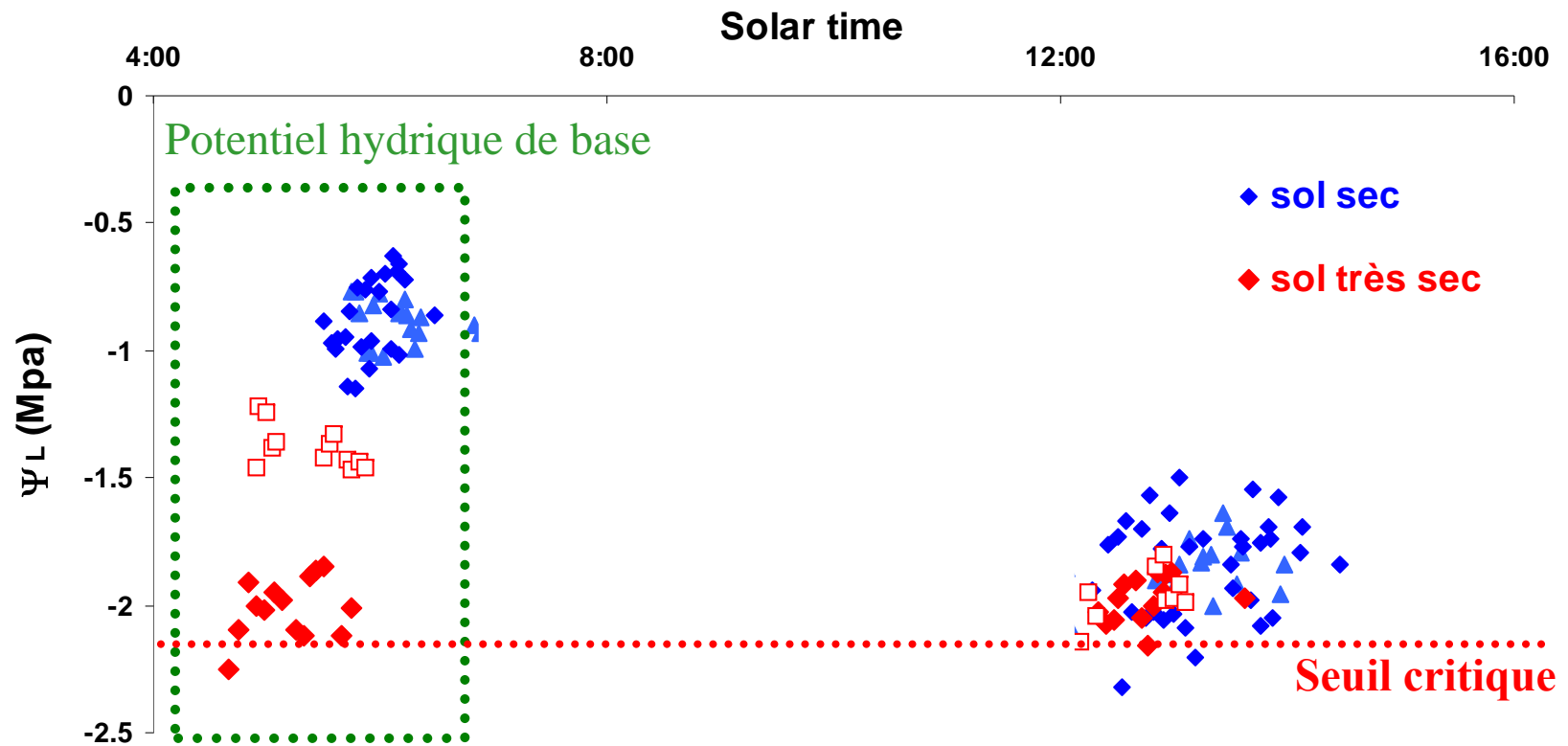
Stomatal conductance vs leaf water potential for piñon (open circles) and juniper (closed circles) at Mesita del Buey, Los Alamos, New Mexico. Data from Barnes (1986).

La réponse à la contrainte hydrique: exemple de comportement anisohydrique



- *Hammada scoparia*, C4
 - But also sunflower or barley
- ré-équilibrage du potentiel avec celui du sol la nuit .
- L'écart Ψ nuit – Ψ jour est maintenu (pas de régulation)
- Pression de turgescence négative (plasmolyse) (tolérance)

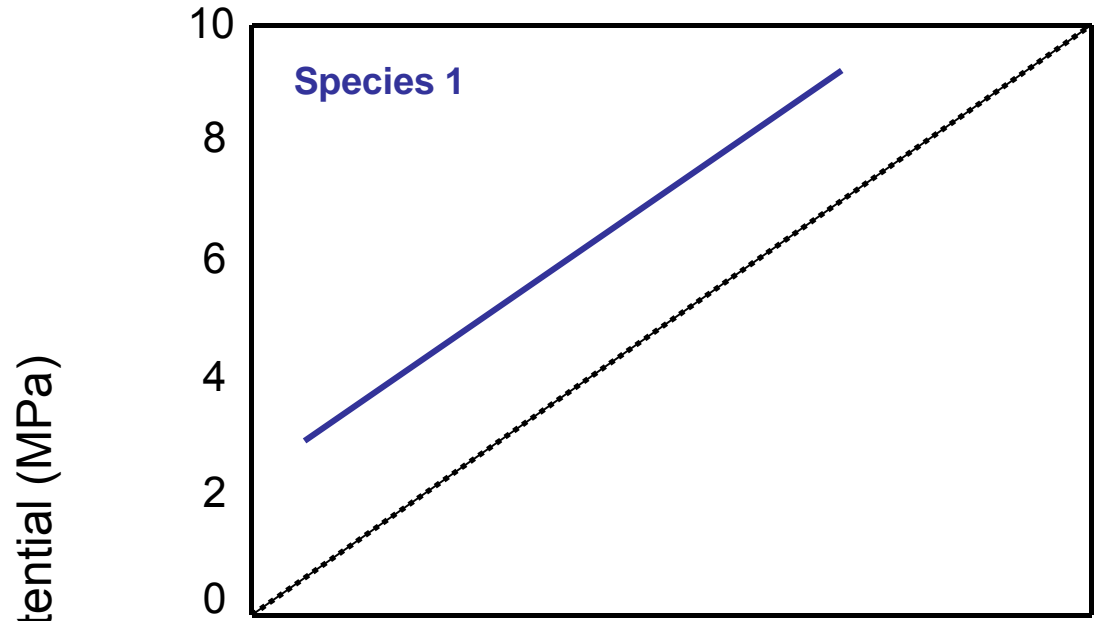
La réponse à la contrainte hydrique: comportement isohydrique et croissance en dimension chez le Pin maritime



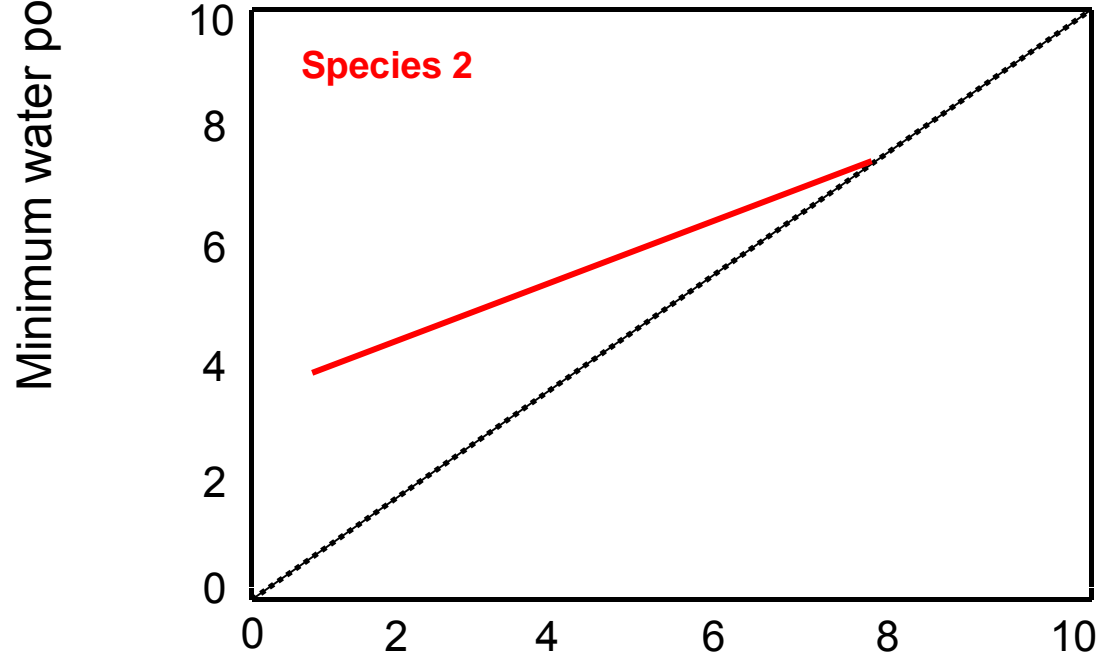
La réponse à la contrainte hydrique:

comportement isohydrique et croissance en dimension
chez le Pin maritime

- *Pinus pinaster*, C3 (autres : maize, pitch, and poplar)
- ré-équilibrage du potentiel avec celui du sol la nuit .
- L'écart Ψ nuit – Ψ jour diminue (régulation stomatique)
- Pression de turgescence reste ≥ 0 (prévention)



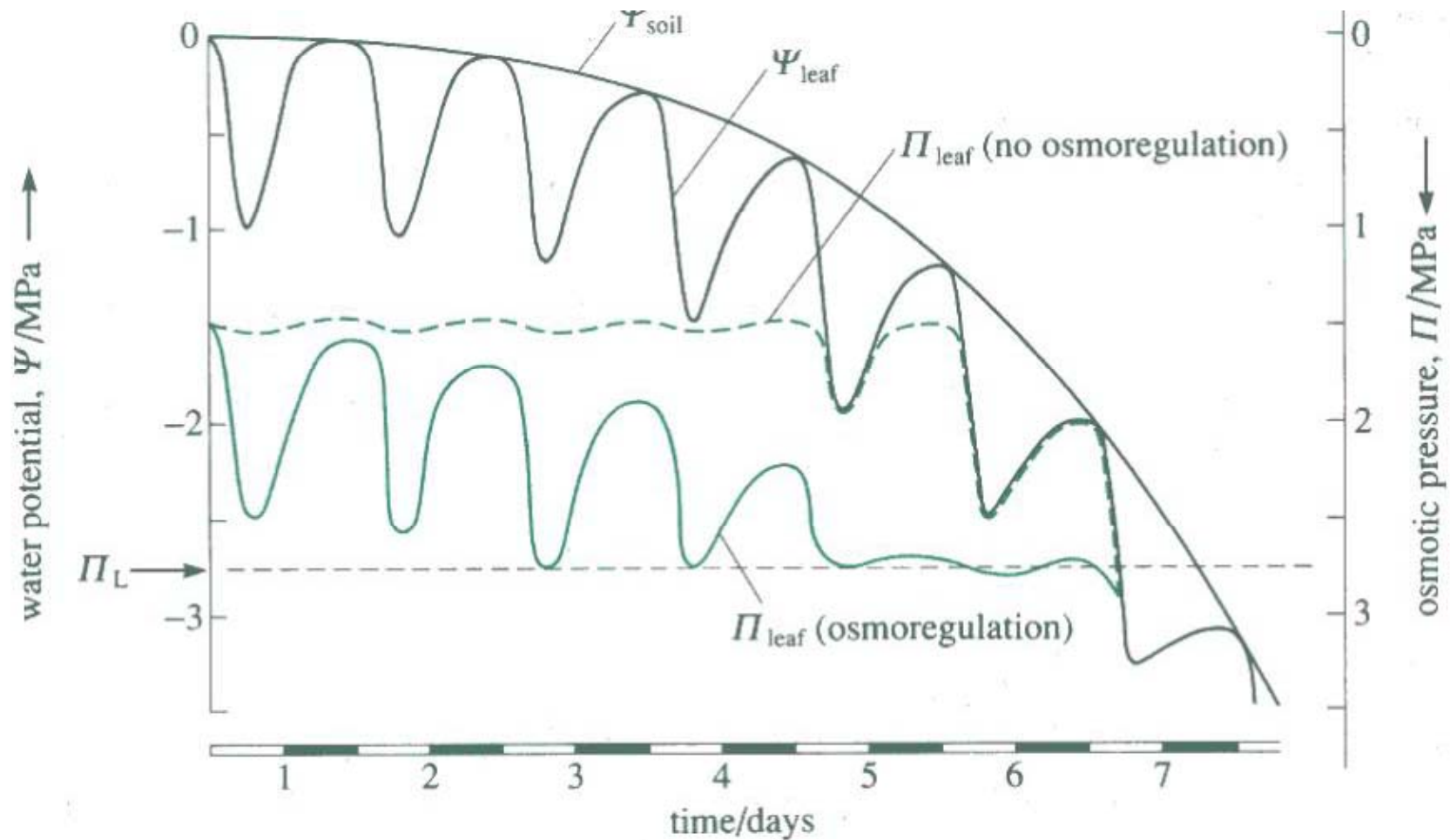
Anisohydrique



Isohydrique

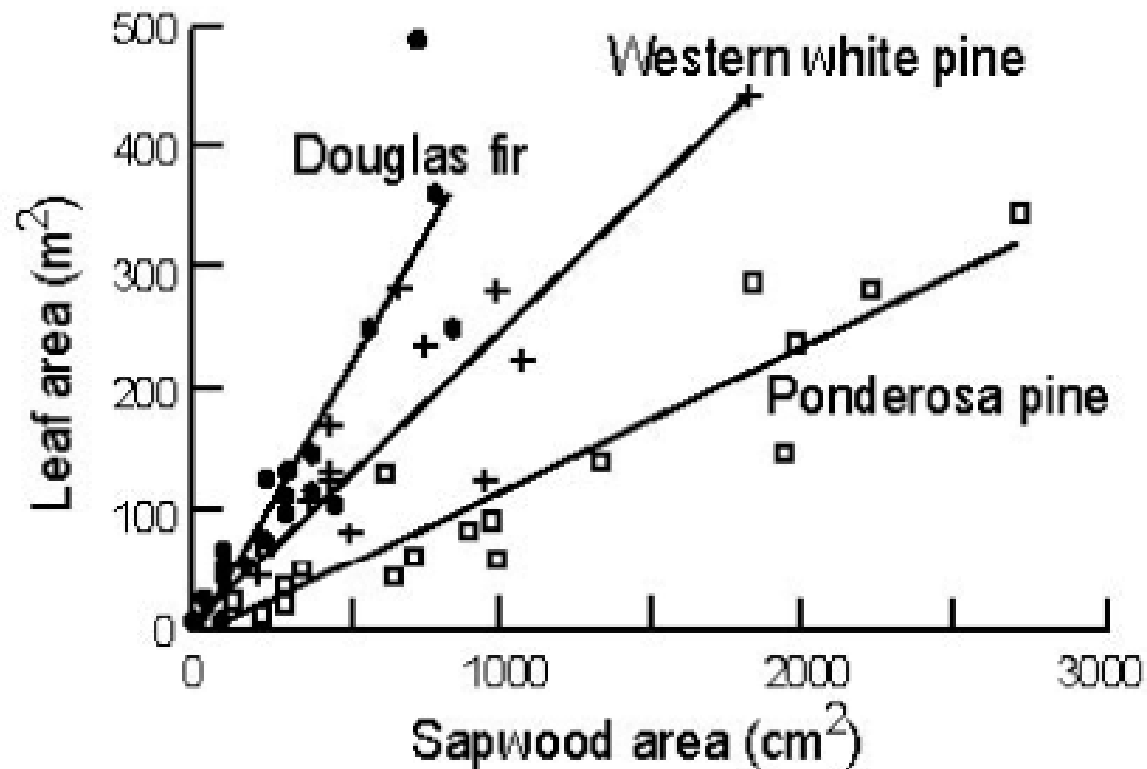
Predawn water potential (MPa)

Osmorégulation



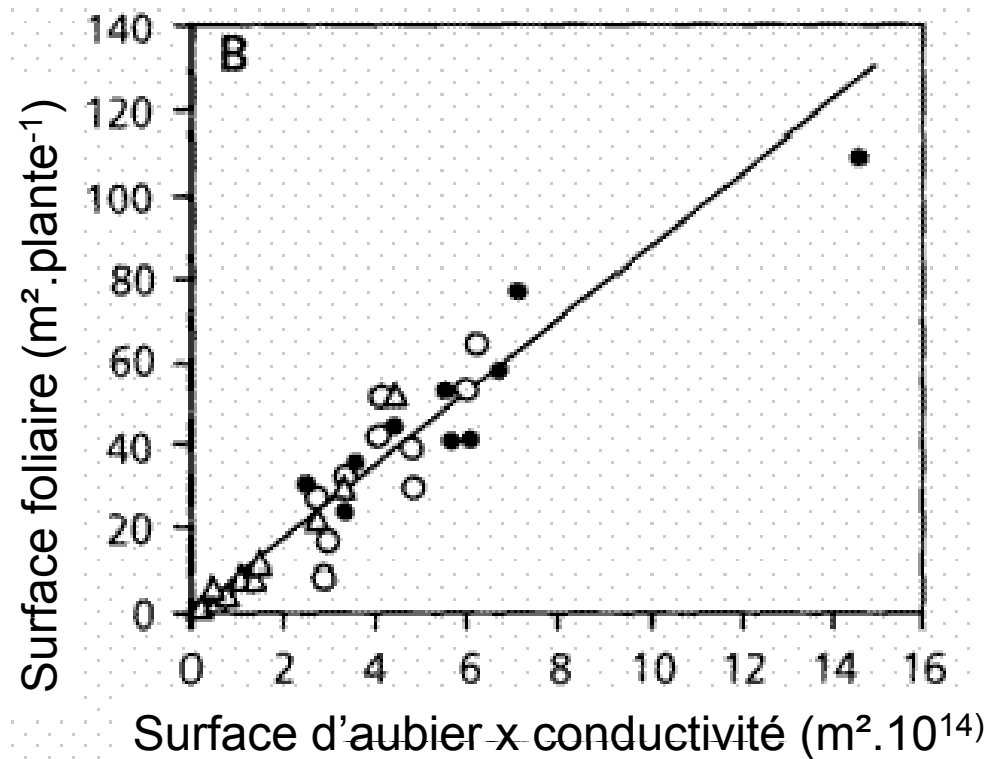
Phénomène fréquent chez les plantes (betterave sucrière) mais pas universel ; comme la vigne

Adaptation du fonctionnement intégré de l'arbre entier



- La relation surface foliaire – capacité conductrice exprime l'intégration du fonctionnement hydraulique au niveau de l'arbre entier.
- Elle dépend de la conductivité spécifique du Xylème.
- Les plantes de milieu aride ont un rapport feuille / aubier plus faible.

Adaptation du fonctionnement intégré de l'arbre entier



La relation surface foliaire – capacité conductrice exprime l'intégration du fonctionnement hydraulique de la plante.

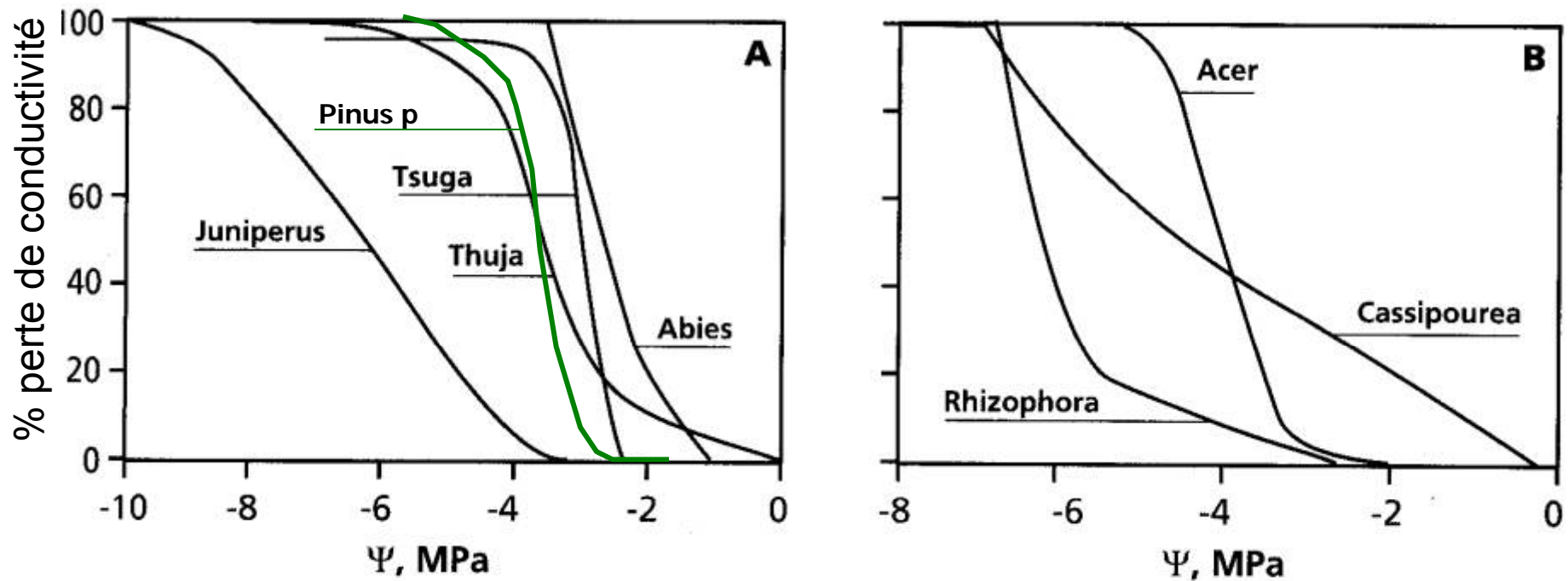
Adaptation du fonctionnement intégré de la plante

Rapport surface foliaire / surface d'aubier (A_f/A_s) d'espèces conifères classées suivant l'aridité du milieu

Species	Common name	$A_f:A_s$ ($m^2 m^{-2}$)
Mesic environments		
<i>Abies balsamea</i>	Balsam fir	6700–7100
<i>A. amabilis</i>	Pacific silver fir	6300
<i>A. grandis</i>	Grand fir	5100
<i>A. lasiocarpa</i>	Subalpine fir	7500
<i>Larix occidentalis</i>	Western larch	5000
<i>Picea abies</i>	Norway spruce	4600
<i>P. engelmanni</i>	Engelmann spruce	2900–3400
<i>P. sitchensis</i>	Sitka spruce	4500
<i>Pseudotsuga menziesii</i>	Douglas fir	3800–7000
<i>Tsuga heterophylla</i>	Western hemlock	4600
<i>T. mertensiana</i>	Mountain hemlock	1600
Average		5000 ± 500
Xeric environments		
<i>Juniperus monosperma</i>	One-seeded juniper	800
<i>J. occidentalis</i>	Western juniper	1800
<i>Pinus contorta</i>	Lodgepole pine	1100–3000
<i>P. edulis</i>	Pinyon pine	2500
<i>P. nigra</i>	Austrian pine	1500
<i>P. ponderosa</i>	Ponderosa pine	1900
<i>P. sylvestris</i>	Scotch pine	1400
<i>P. taeda</i>	Loblolly pine	1300–3000
Average		1800 ± 200

Source: Margolis et al. 1995.

Courbes de vulnérabilité à la cavitation



← Milieux plus arides
Xylème plus « coûteux »
Croissance plus lente

Pousser vite, être grand *versus* préserver son xylème.

Conifères: le genévrier (Juniper) est moins vulnérable que le sapin (Abies)

Feuillus: *Acer* est plus vulnérable que la mangrove (*Rhizophora*)

Le compromis hydraulique

efficacité – vulnérabilité – support méca.

TABLE 6. Hydraulic conductance of xylem conduits, maximum velocity of water transport through the conduits and xylem diameter for stems of different types of plants.

	Hydraulic conductivity of xylem lumina ($\text{m}^2 \text{s}^{-1} \text{MPa}^{-1}$)	Maximum velocity (mm s^{-1})	Vessel diameter μm
Evergreen conifers	5–10	0.3–0.6	<30
Mediterranean sclerophylls	2–10	0.1–0.4	5–70
Deciduous diffuse porous	5–50	0.2–1.7	5–60
Deciduous ring porous	50–300	1.1–12.1	5–150
Herbs	30–60	3–17	
Lianas	300–500	42	200–300

- La conductivité augmente avec la puissance 4 du diamètre d'un cylindre.
- La conductivité du xylème dépend plus du diamètre des ponctuations que de celui des vaisseaux (trachéides)
- bois poreux > bois diffus > conifères
- La tige d'une liane a la même conductivité qu'un tronc de section 10 x plus importante.

Vulnérabilité à la cavitation

Vulnérabilité du système conducteur à l'embolie liée à la sécheresse : Ψ_{50}

TABLE 2. Vulnerability to xylem cavitation (Ψ_{50} , MPa) and specific conductivity (K_s ; $\text{kg}\cdot\text{m}^{-1}\cdot\text{MPa}^{-1}\cdot\text{s}^{-1}$) for the various functional groups included in this study (means \pm 1 SE).

Functional group	Cavitation			Conductivity		
	Ψ_{50}	MAP (mm)	<i>n</i>	K_s	MAP (mm)	<i>n</i>
Angiosperms						
Winter deciduous shrubs	-2.66	140	2	1.57	140	2
Winter deciduous trees	-2.34 \pm 0.17	768 \pm 62	46	1.58 \pm 0.22	777 \pm 85	30
Drought deciduous shrubs	-4.47 \pm 0.64	196 \pm 23	9	1.55 \pm 0.68	166 \pm 26	5
Drought deciduous trees	-2.13 \pm 0.48	1383 \pm 387	5	0.96 \pm 0.22	1383 \pm 387	5
Evergreen shrubs	-5.09 \pm 0.54	761 \pm 175	21	1.75 \pm 0.74	434 \pm 118	8
Evergreen trees	-1.51 \pm 0.23	2610 \pm 152	44	2.43 \pm 0.62	1539 \pm 247	12
Gymnosperms						
Conifer shrubs	-8.95 \pm 1.81	511 \pm 174	5	0.24	465	2
Conifer trees	-4.17 \pm 0.33	984 \pm 136	34	0.48 \pm 0.05	817 \pm 103	22

Notes: Mean (\pm 1 SE) annual precipitation (MAP) and sample size (*n*) for each group and variable combination are included for comparison. Standard errors were not calculated for those groups with *n* < 3.

**Le compromis hydraulique efficacité
– vulnérabilité**

Vulnérabilité à la cavitation

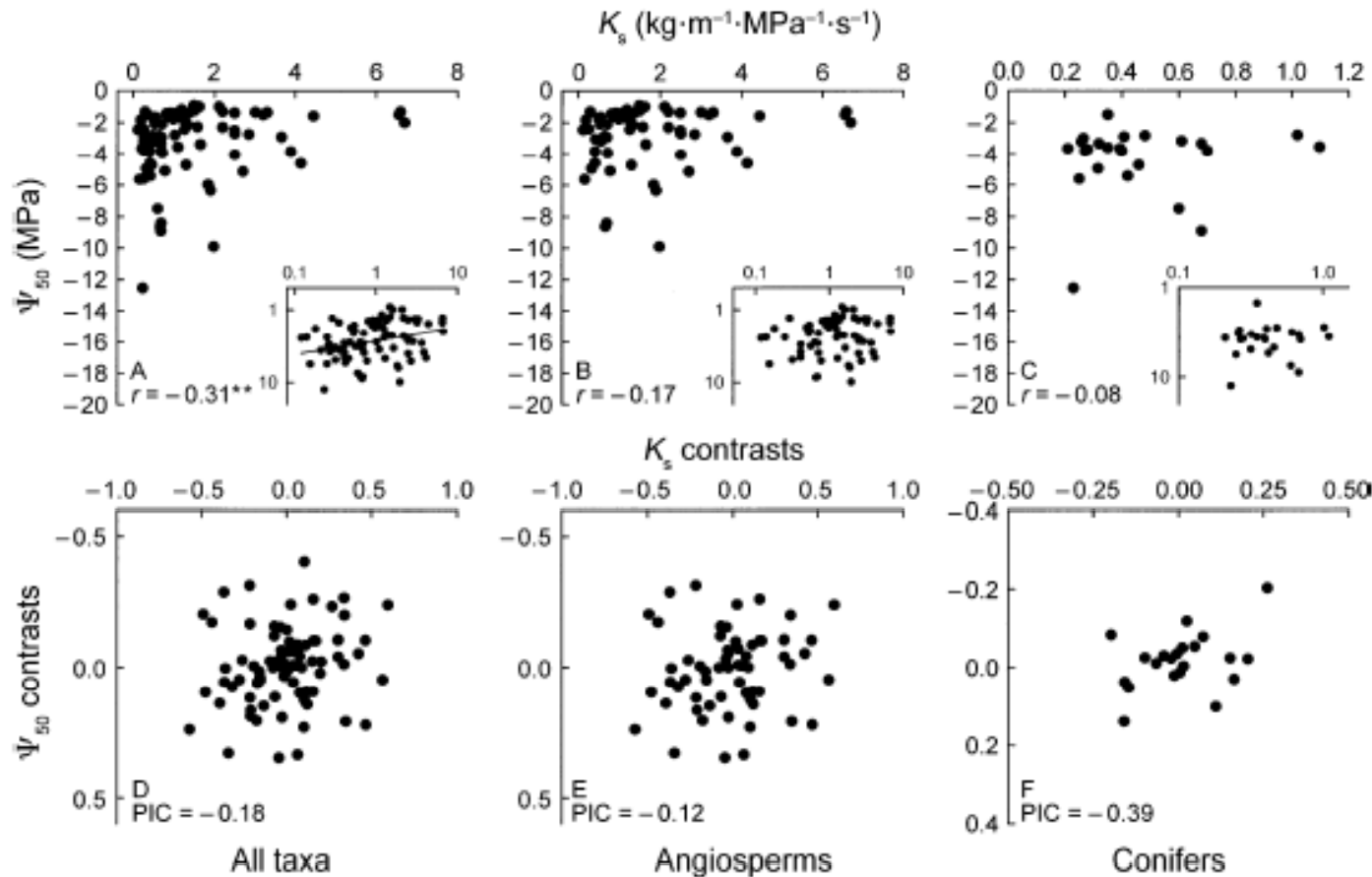
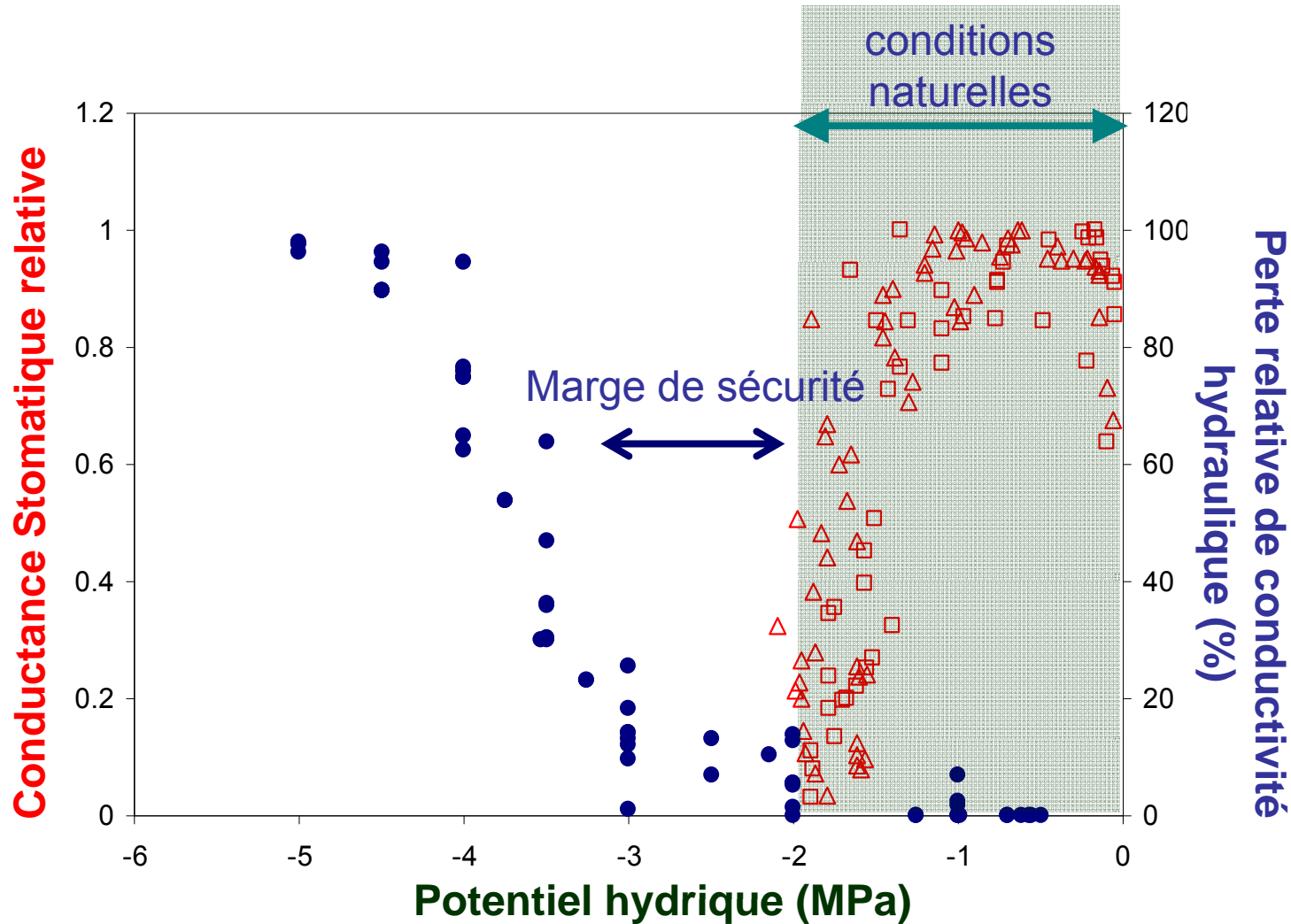


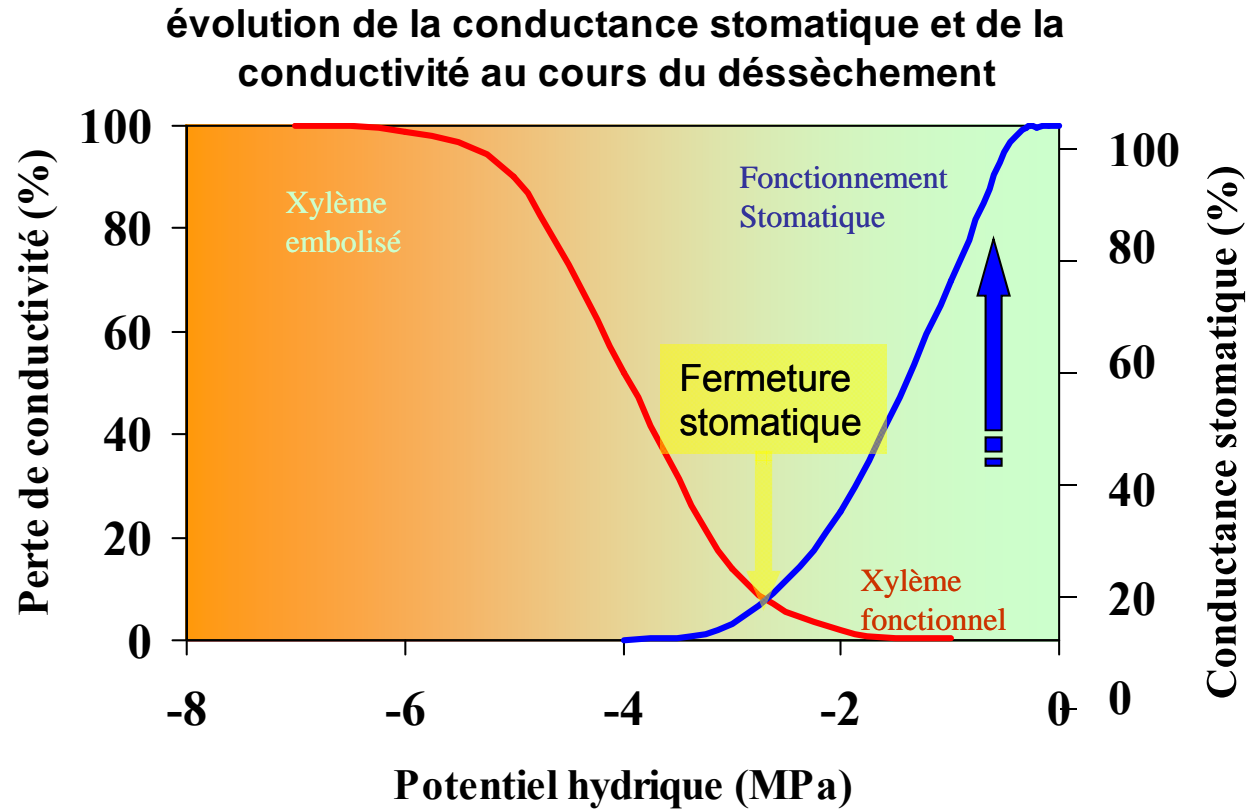
FIG. 6. The relationship between xylem tension at which 50% cavitation occurred (Ψ_{50}) and specific conductivity of xylem (K_s) analyzed using (A, B, C) Pearson correlation coefficients and (D, E, F) independent contrast correlations for all taxa and for angiosperms and conifers considered separately. Angiosperm data were pooled because there were no differences between deciduous and evergreen groups (Table 3). Log-transformed relationships are shown in the insets. For descriptive purposes, statistically significant relationships ($*P < 0.05$; $**P < 0.01$) are fitted with least-squares regression lines. To facilitate log transformation for analysis, Ψ_{50} values were converted from negatives to positives. Although data are plotted to reflect the nontransformed relationships in panels A–C, the sign of the correlation coefficient (both standard cross-species correlations [r] and phylogenetically independent contrast correlations [PIC]) and the independent contrast plots (panels D–F) are based on the log-transformed data (see Table 3).

Le compromis hydraulique efficacité – vulnérabilité n'est pas vérifié à l'intérieur des taxons

La réponse à la contrainte hydrique: comportement évitant chez le Pin maritime (Dulhoste, 2005) esp. isohydrique

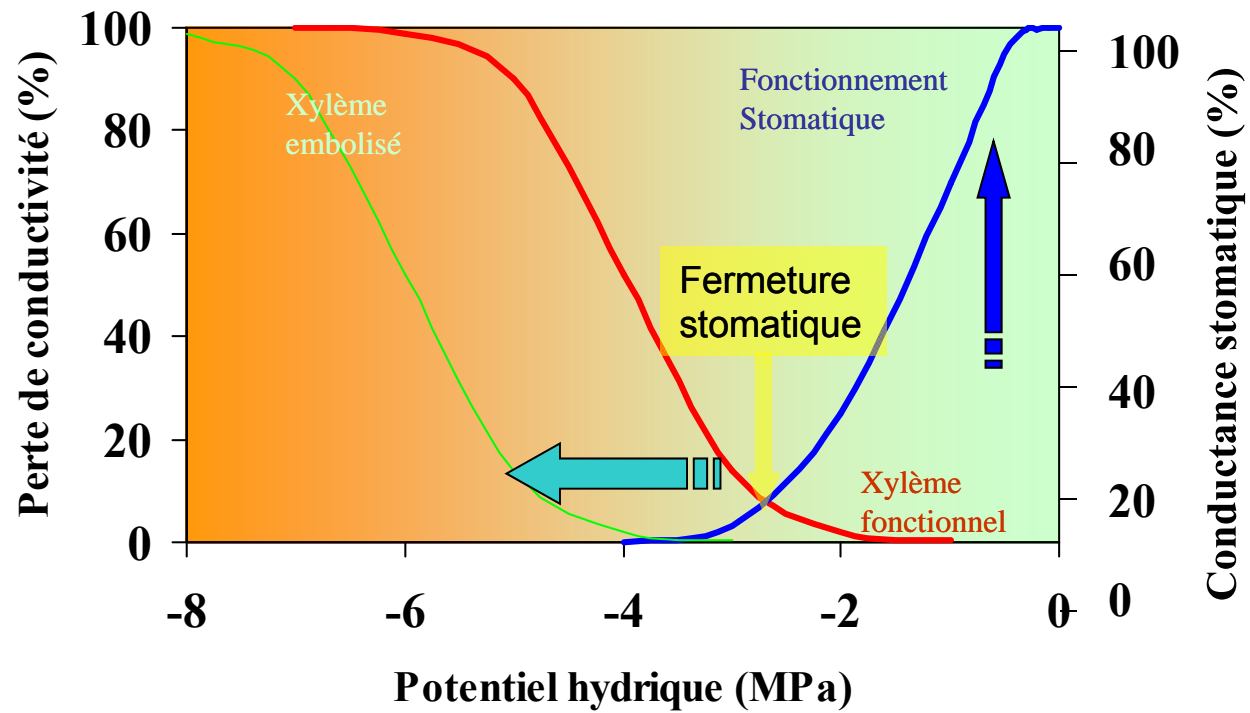


Vulnérabilité à la cavitation et contrôle stomatique

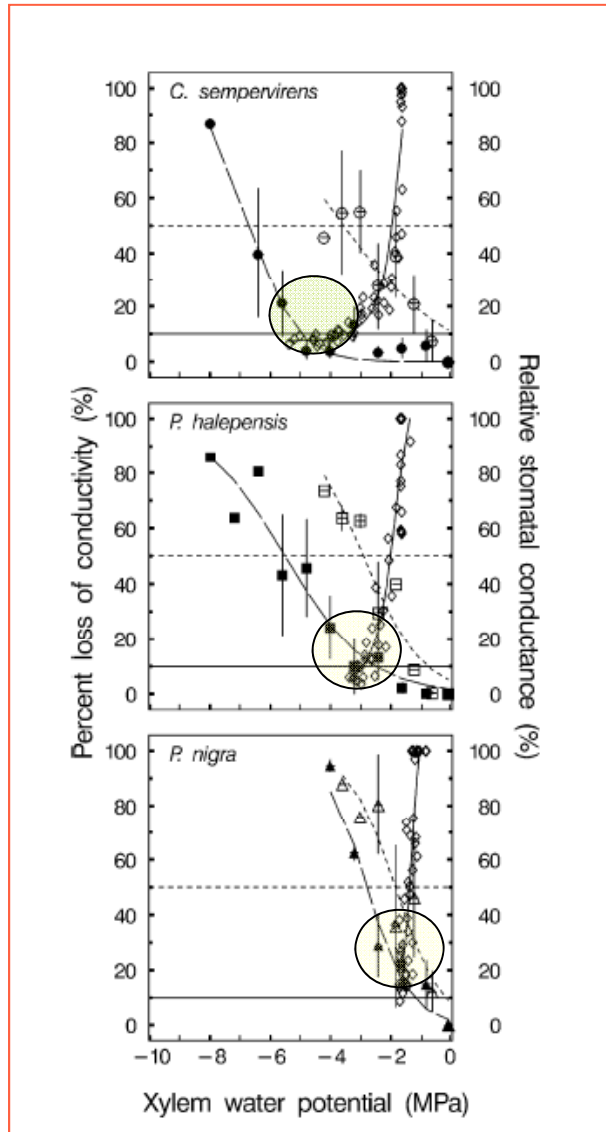


Vulnérabilité à la cavitation et contrôle stomatique

vulnérabilité et contrôle stomatique



Vulnérabilité à la cavitation et fonctionnement stomatique



Courbe de vulnérabilité sur tiges et racines

- cyprès vert
- pin d'Alep
- pin noir

Différences de fonctionnement
coordination
stomate - vulnérabilité

La réponse à la contrainte hydrique

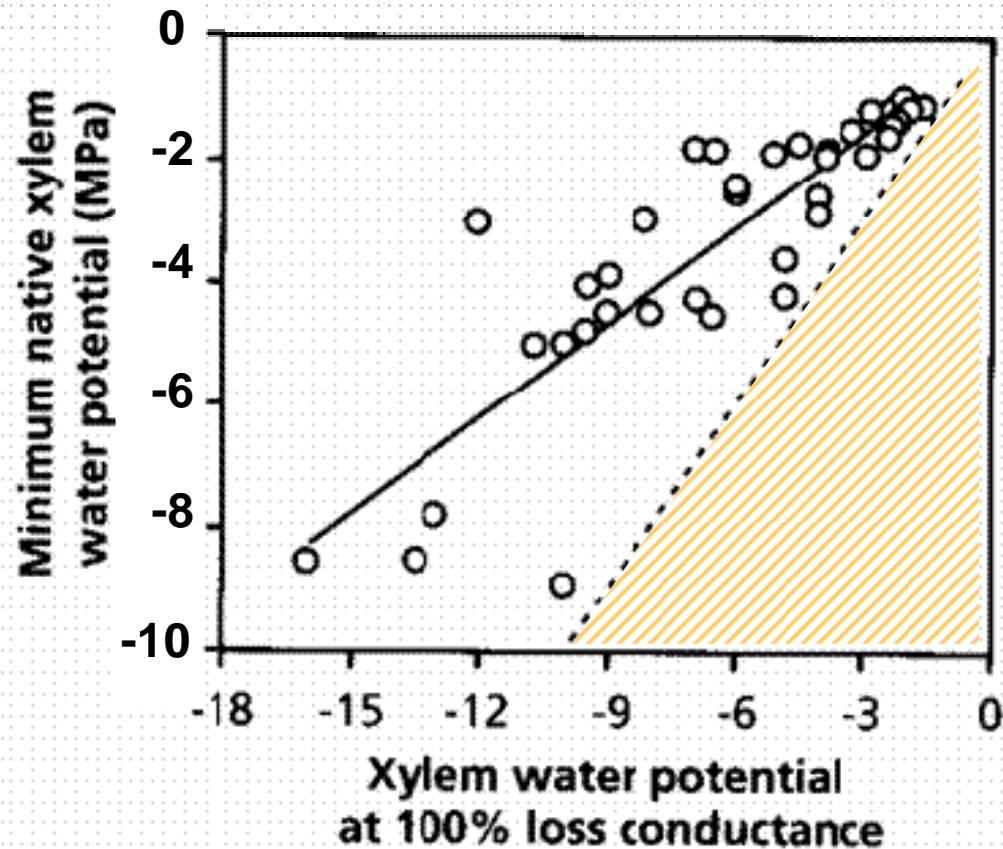


FIGURE 20. Xylem pressure required to induce 100% cavitation versus minimum pressure observe in the field. Dashed line indicates 1:1 relationship. Each point is a different species (Sperry 1995). Copyright Academic Press, Ltd.

Species from dry habitats, which experience negative water potentials for months operate with a much larger safety margin (Sperry 1995)

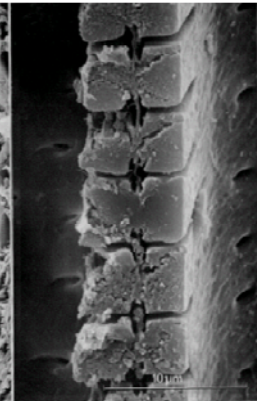
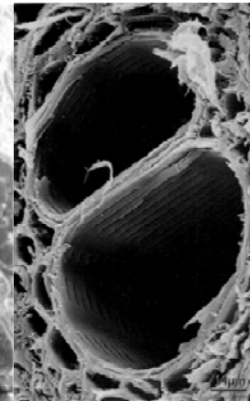
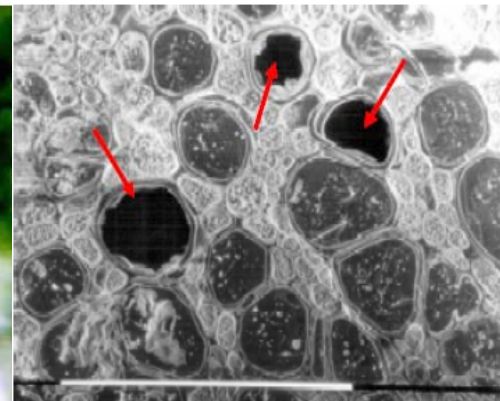
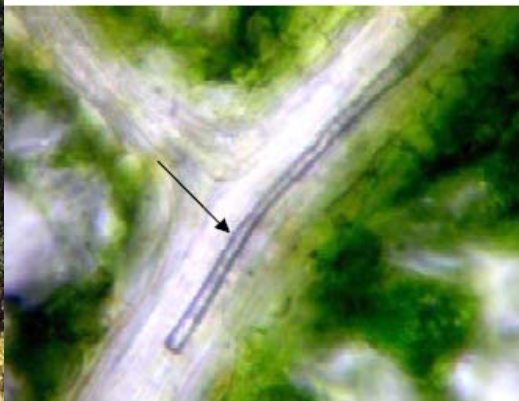
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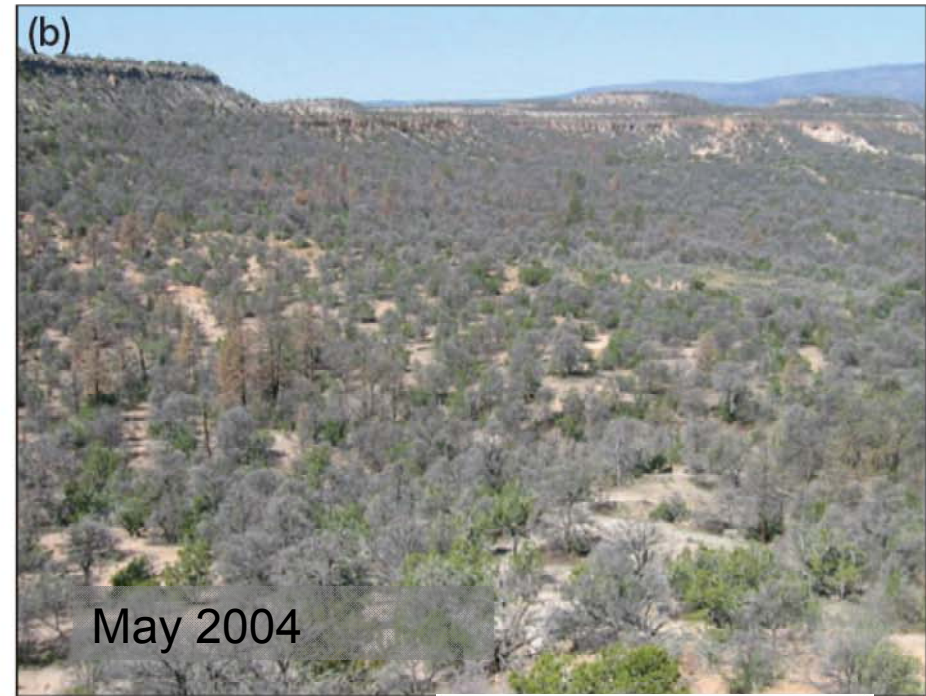
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Story II. Mechanisms of plants survival and mortality during drought



Drought-induced forest dieback



Breshears et al 2009

Juniperus monosperma

Pinus edulis



Why do some plants survive while others succumb to drought?

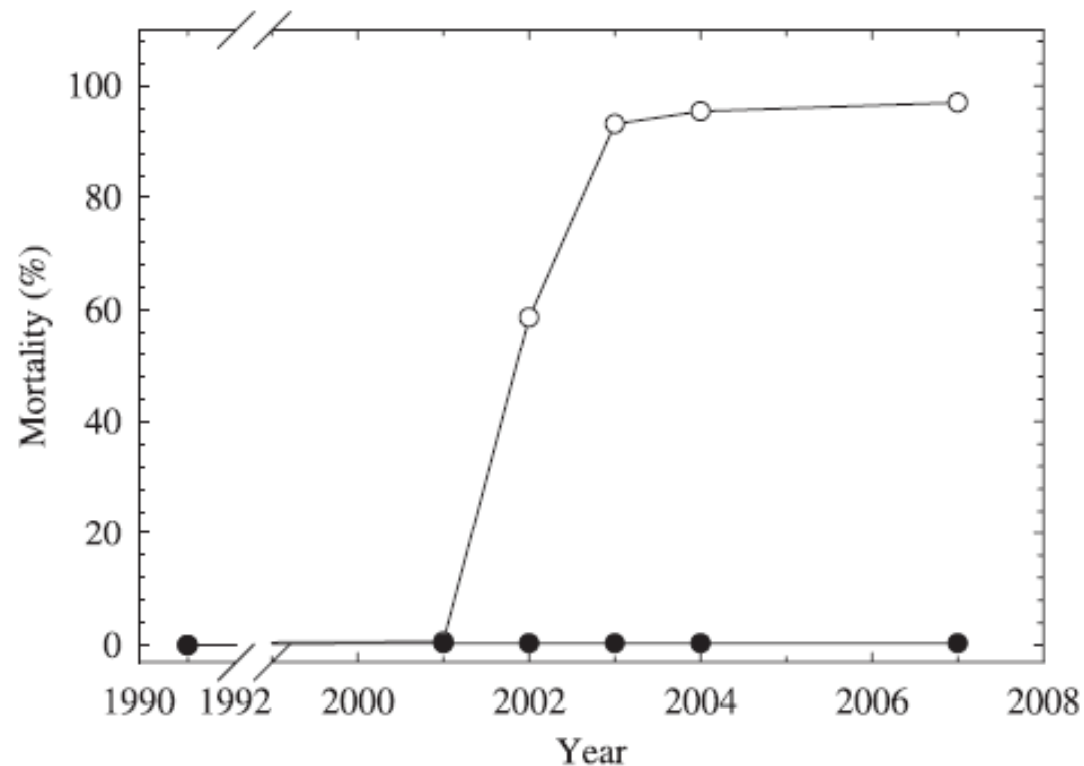
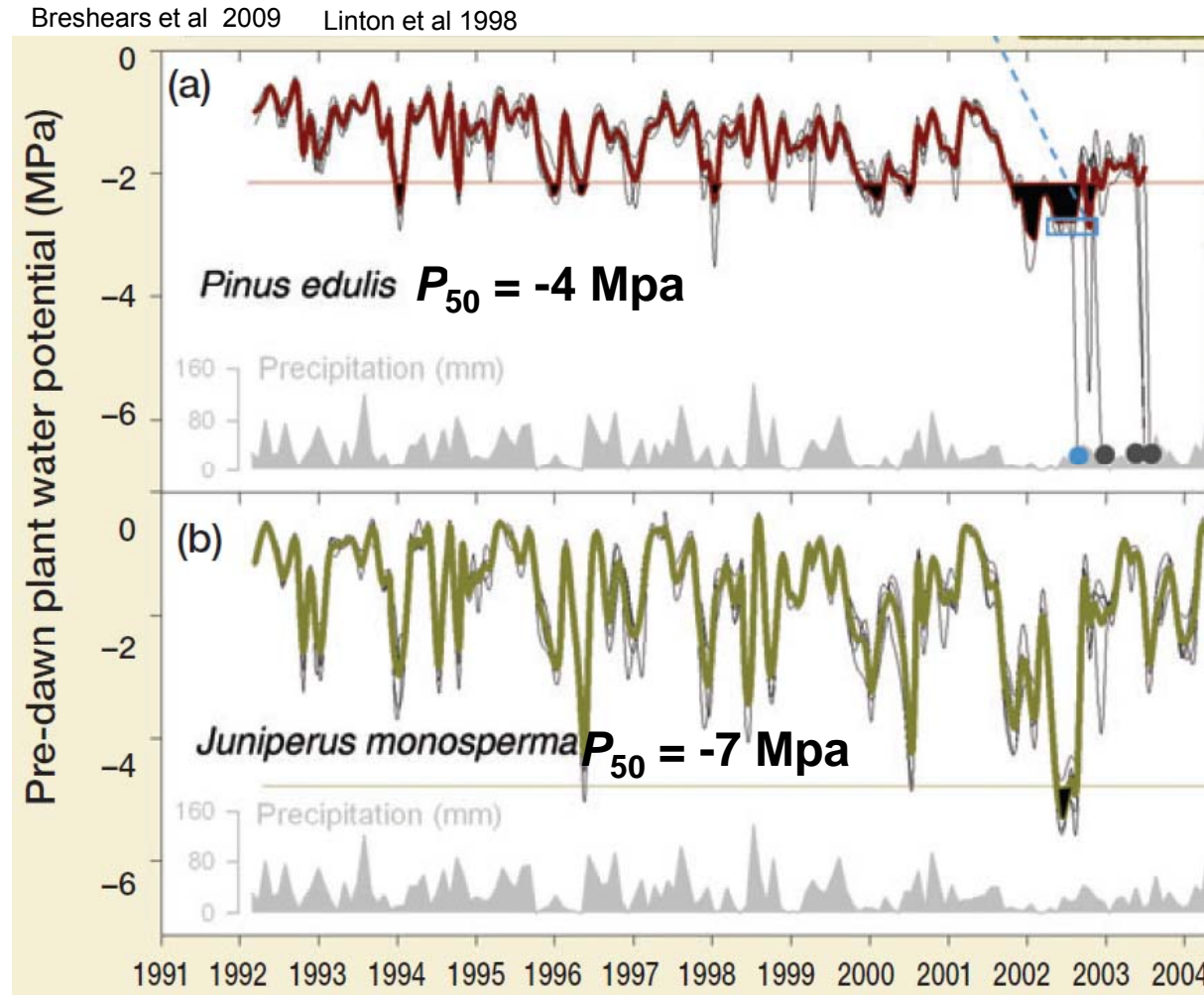


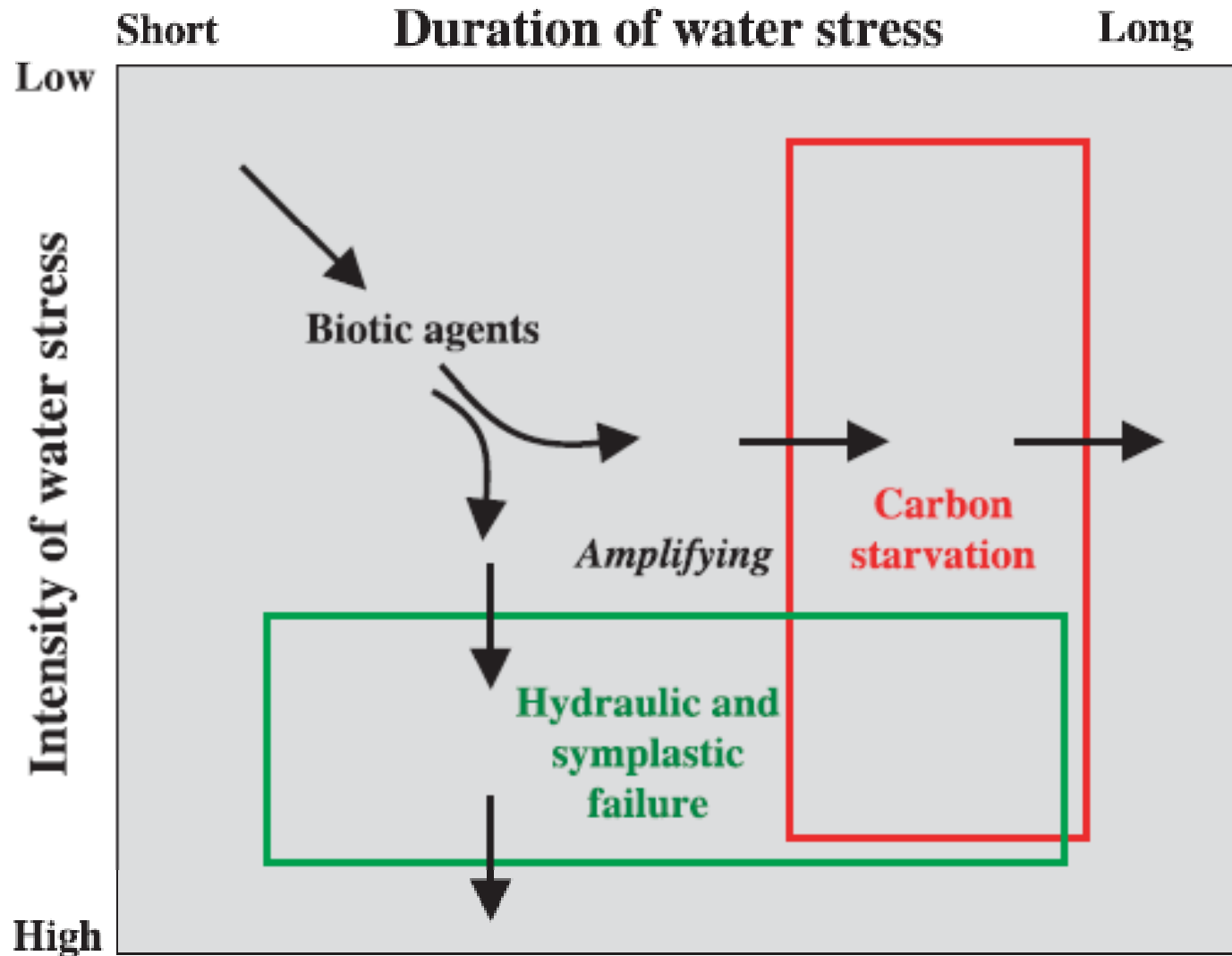
Fig. 2 Percentage mortality of piñon (open circles) and juniper (closed circles) trees at a 1.5 ha site, Mesita del Buey, near Los Alamos, New Mexico. For piñon, 16 of 484 trees survived (97% mortality), whereas for juniper, 559 out of 561 trees survived (< 1% mortality).

Drought-induced forest dieback

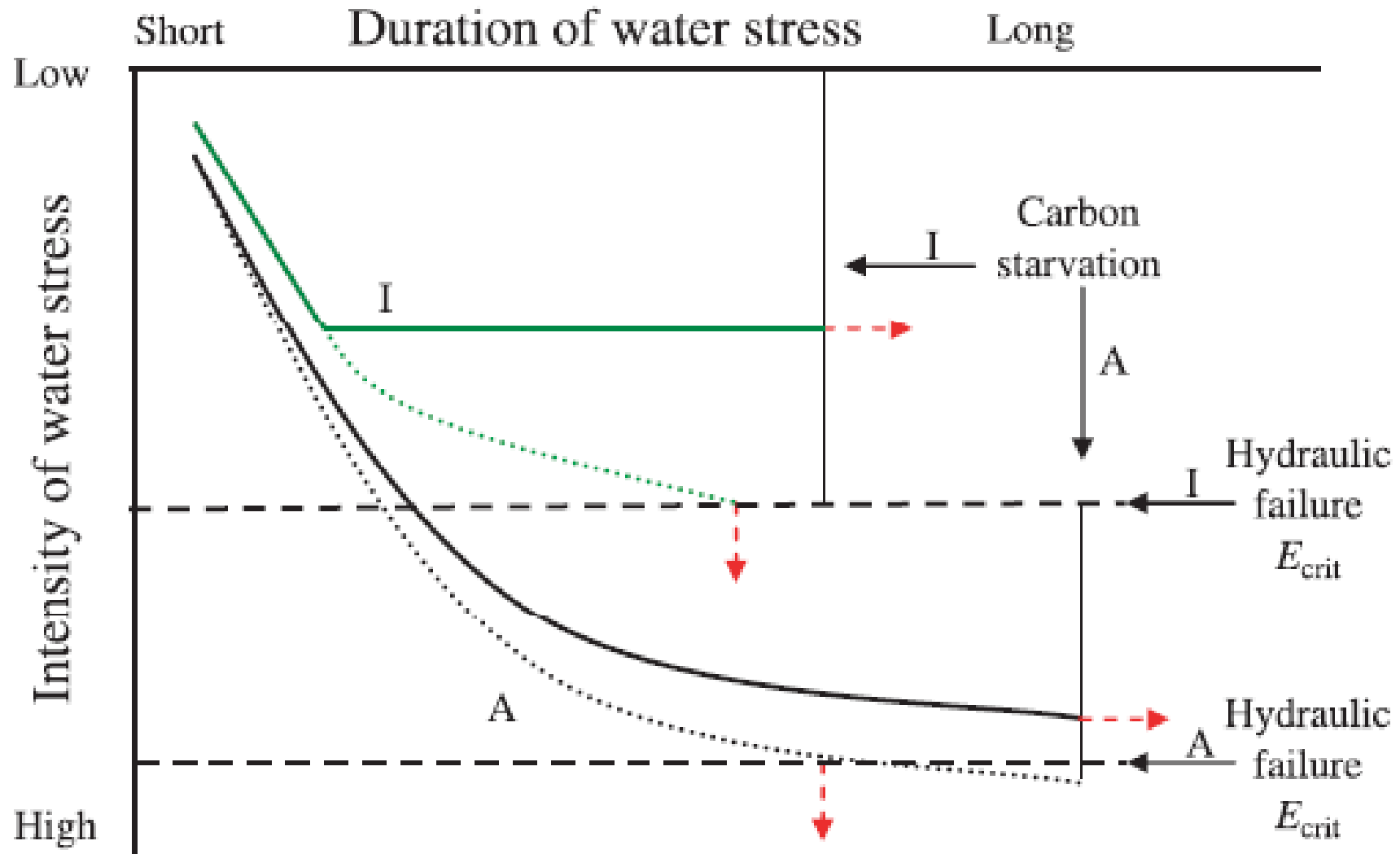


Mortality by hydraulic failure *per se*?

Hypotheses on mechanisms of drought-related mortality related to the intensity and duration of water stress

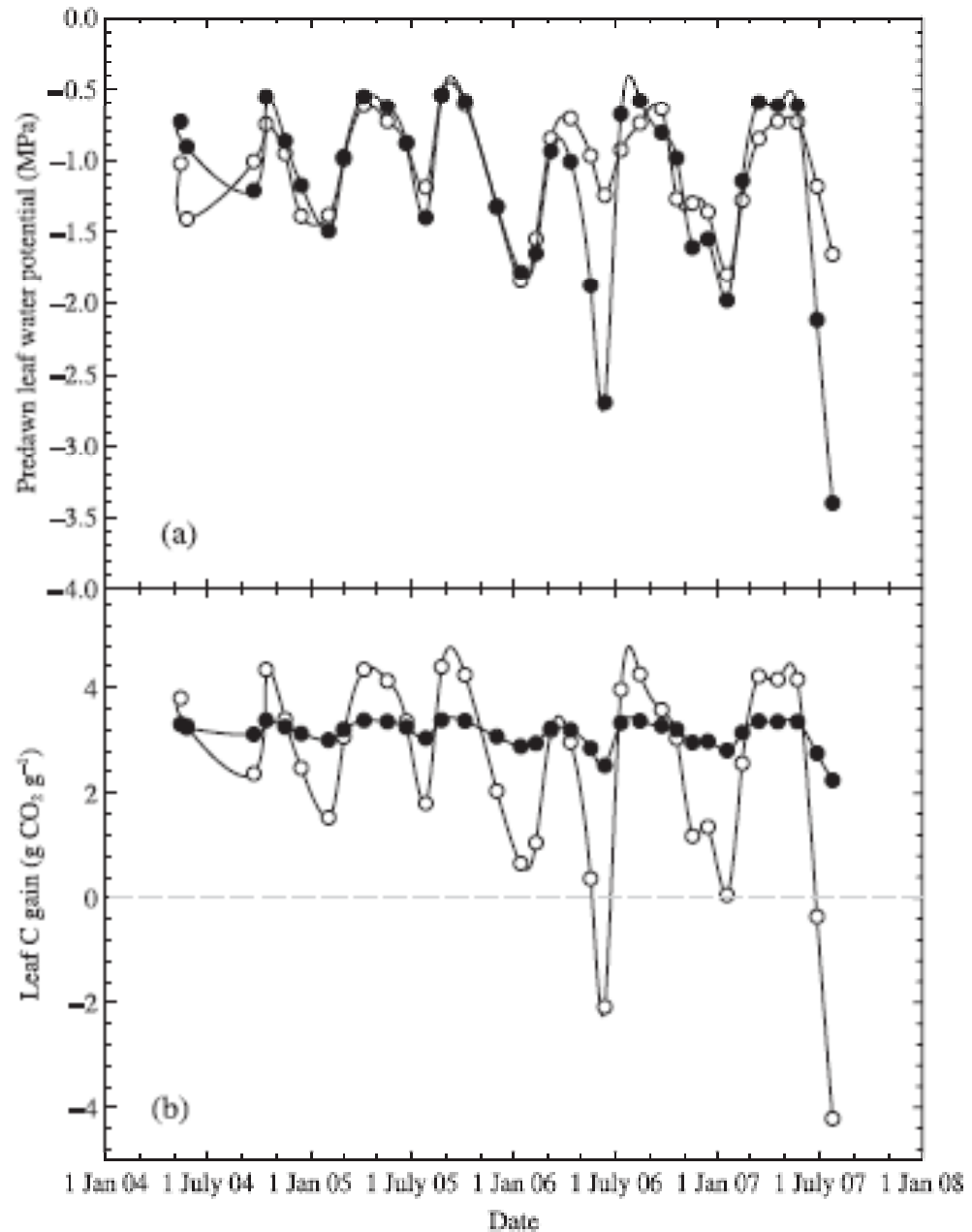


Theoretical predictions of the mechanisms of drought-related mortality for species utilizing isohydric vs anisohydric regulation of water potential.



Carbon starvation

Three years of monthly observations of predawn water potential of piñon (open circles) and juniper (closed circles) from Mesita del Buey, Los Alamos, New Mexico.



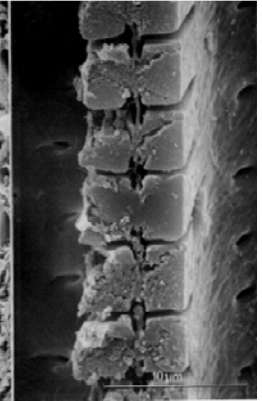
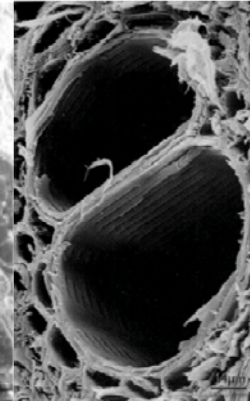
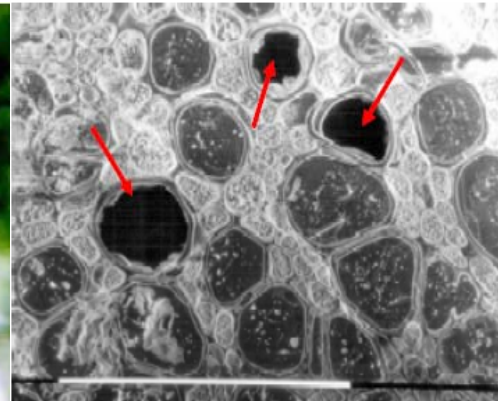
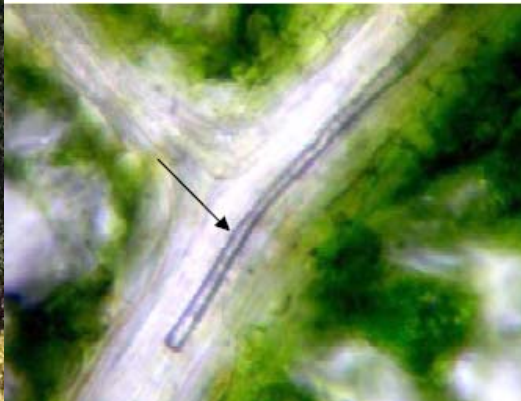
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Story III. Cavitation resistance, survival and species distribution?



1. Survival and cavitation resistance



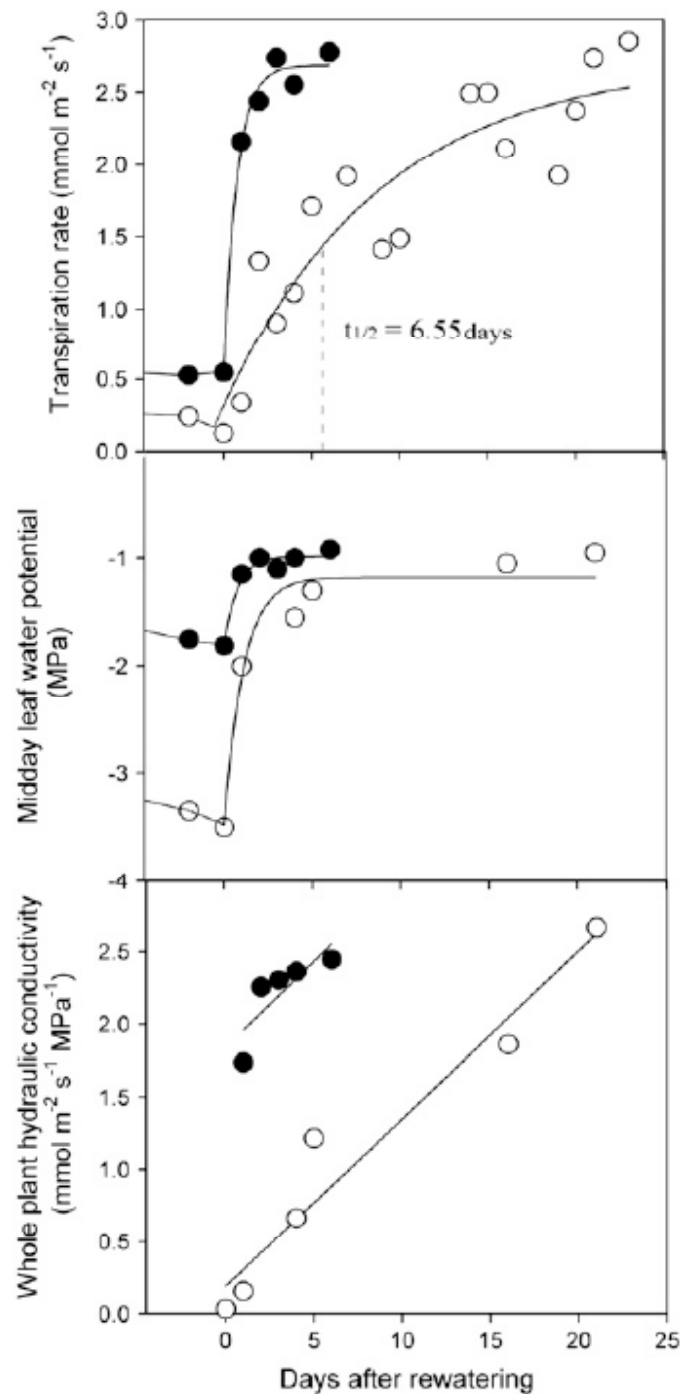
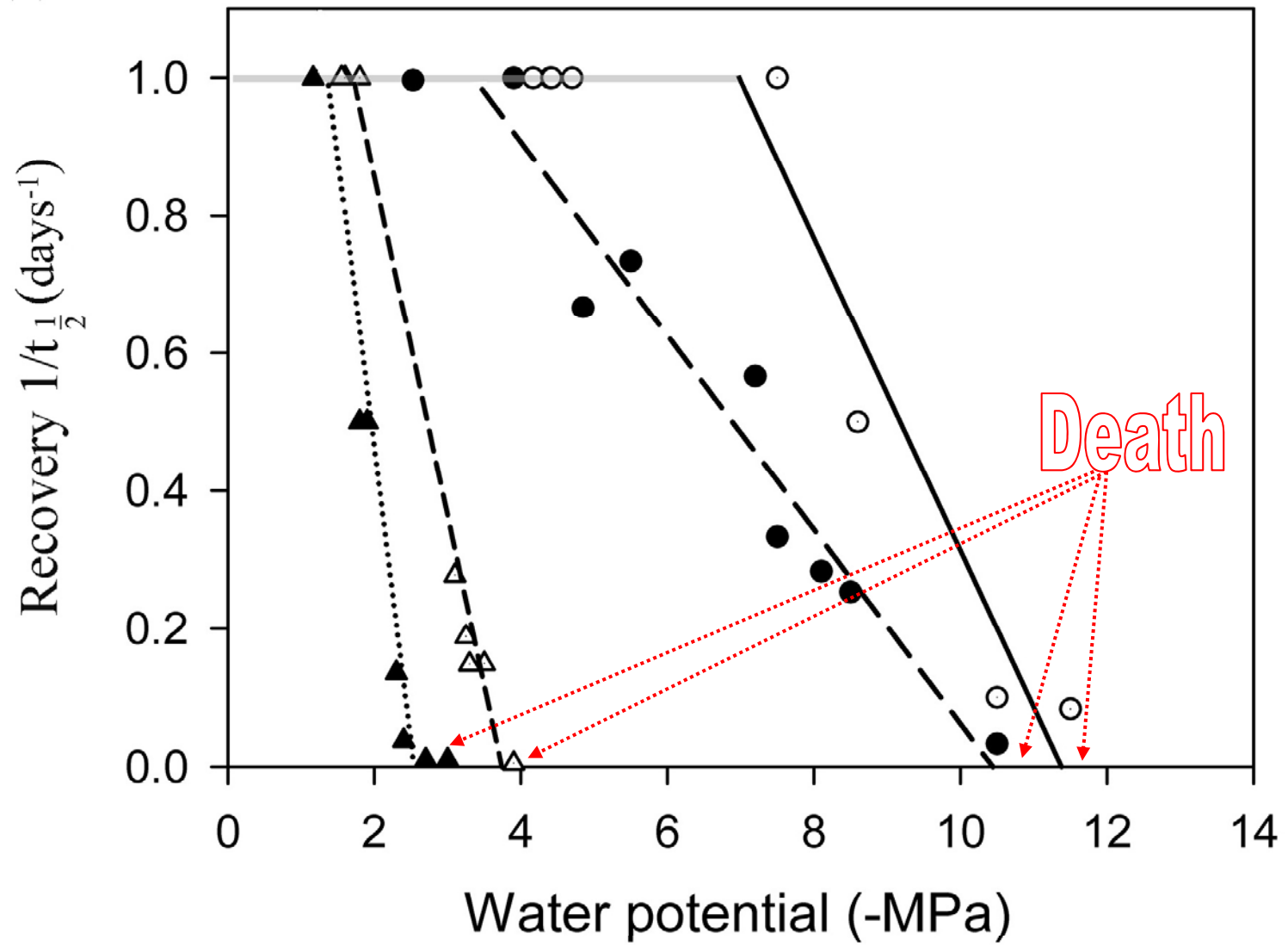
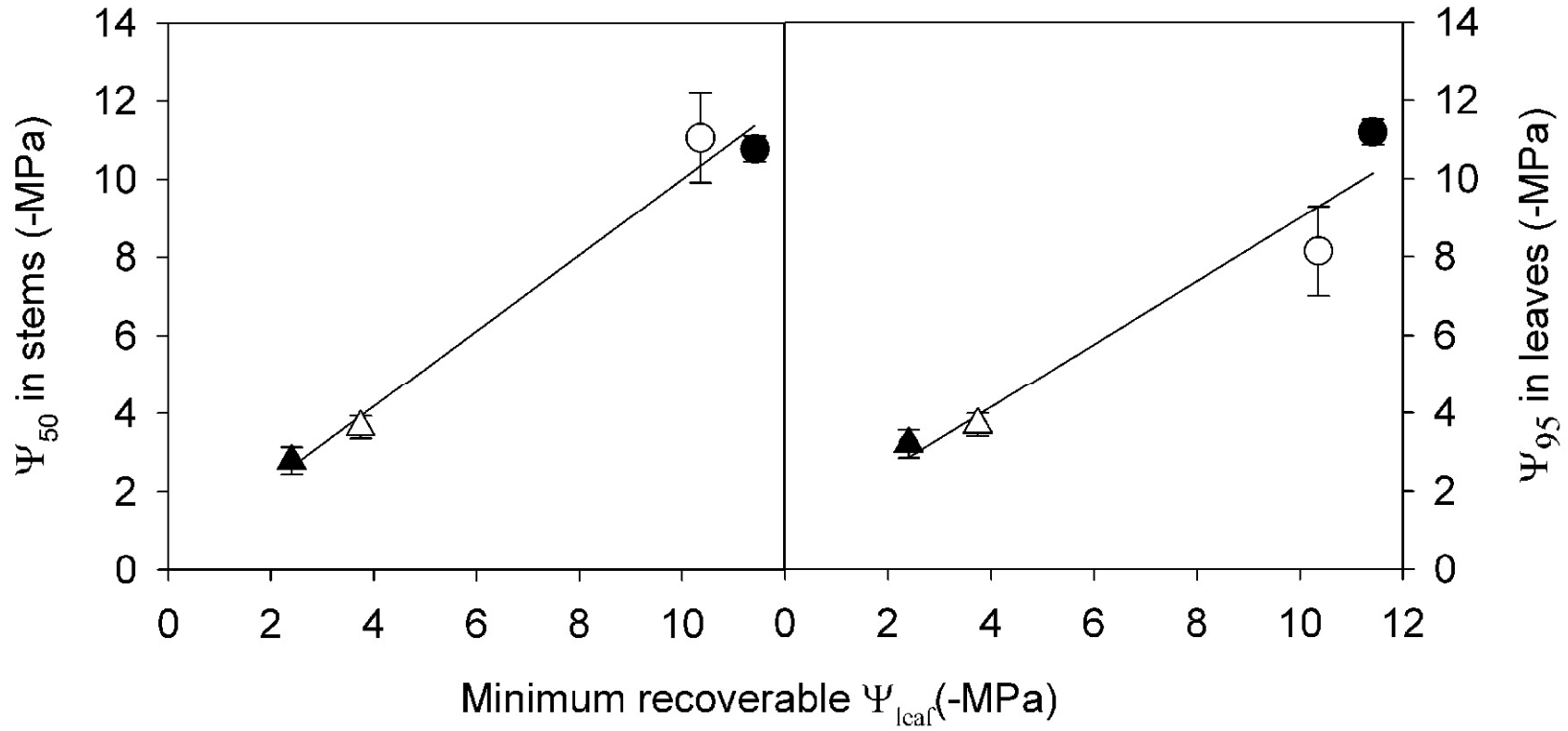


Figure 4. An example of recovery from mild (black circles) and severe (white circles) water stress in rewatered plants of *L. franklinii*. The mildly stressed plant shows a minimal reduction of K_{plant} and is able to rapidly recover leaf hydration and gas exchange. By contrast the severely stressed plant experiences profound depression of K_{plant} that recovers slowly, thus limiting gas-exchange recovery, which has a $t_{1/2}$ of

(a)

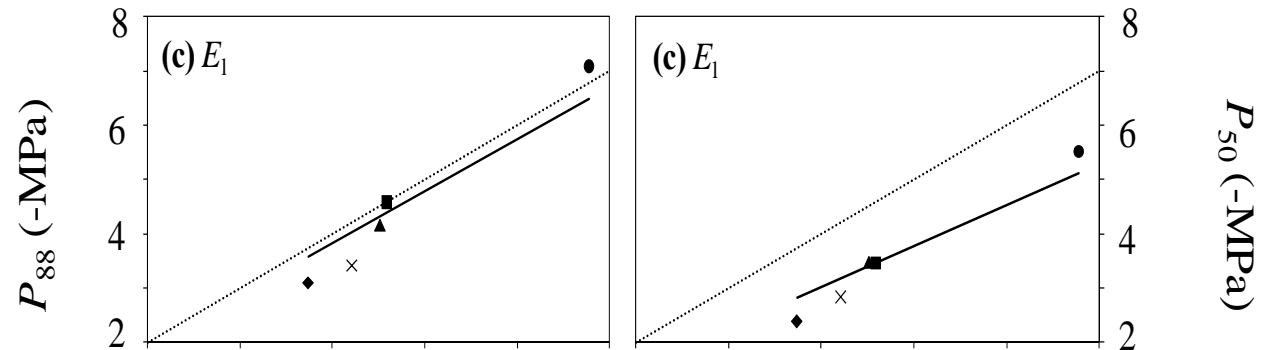


In conifers

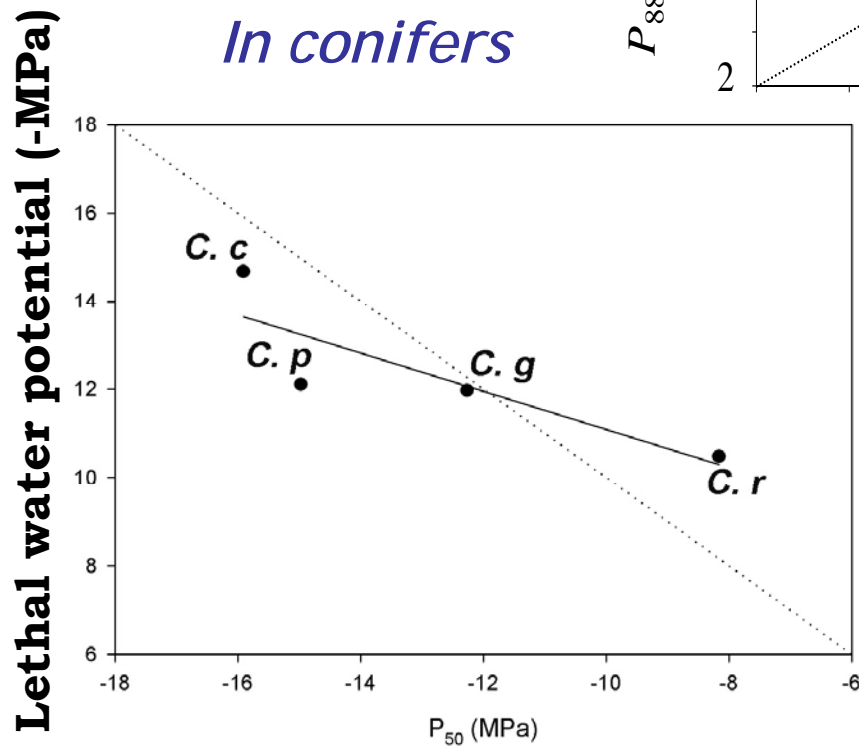


1. Survival, species distribution and cavitation resistance

In angiosperms



In conifers



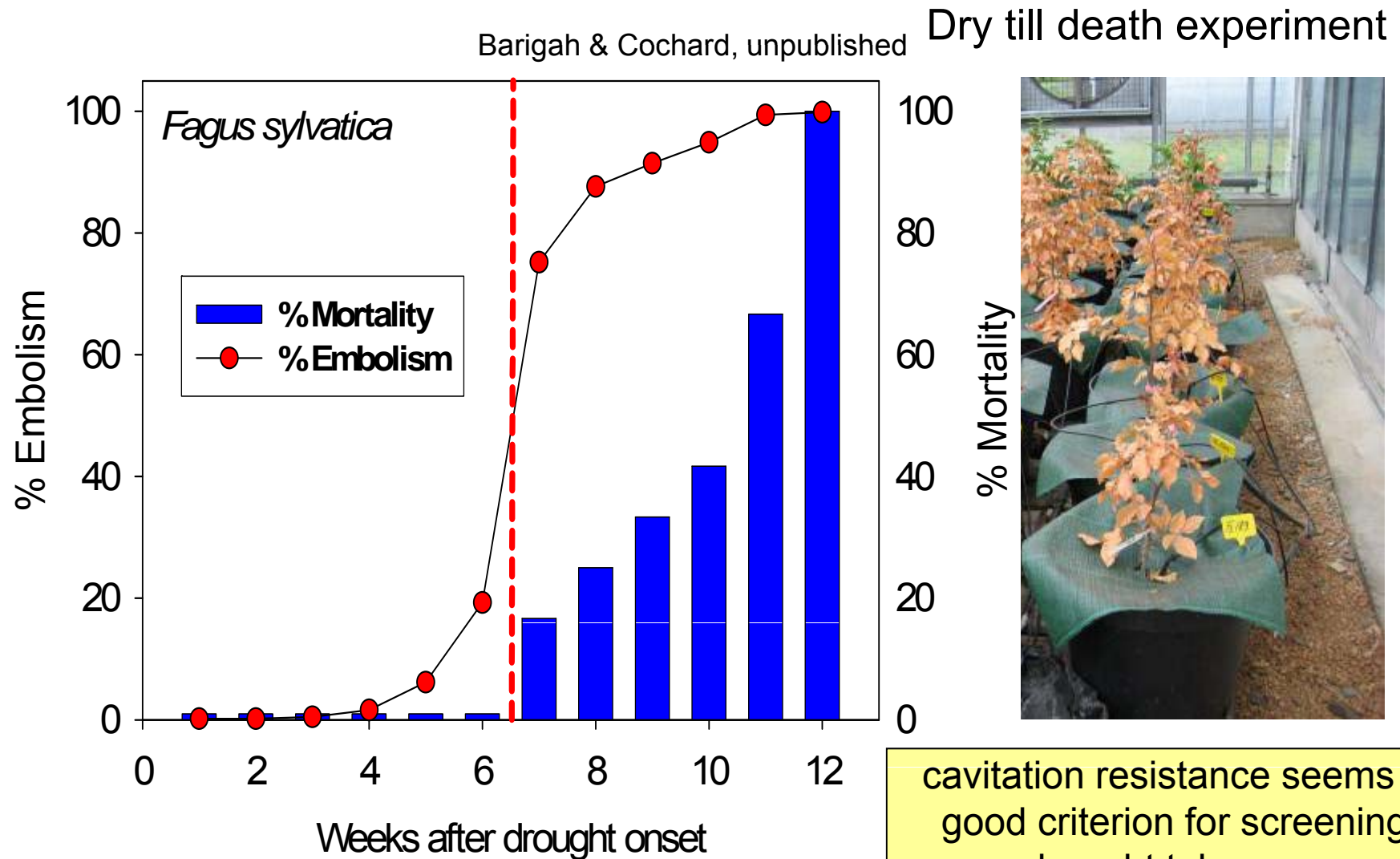
Min recoverable water potential

Urli et al. submitted

Brodribb et al. 2010 New Phytol

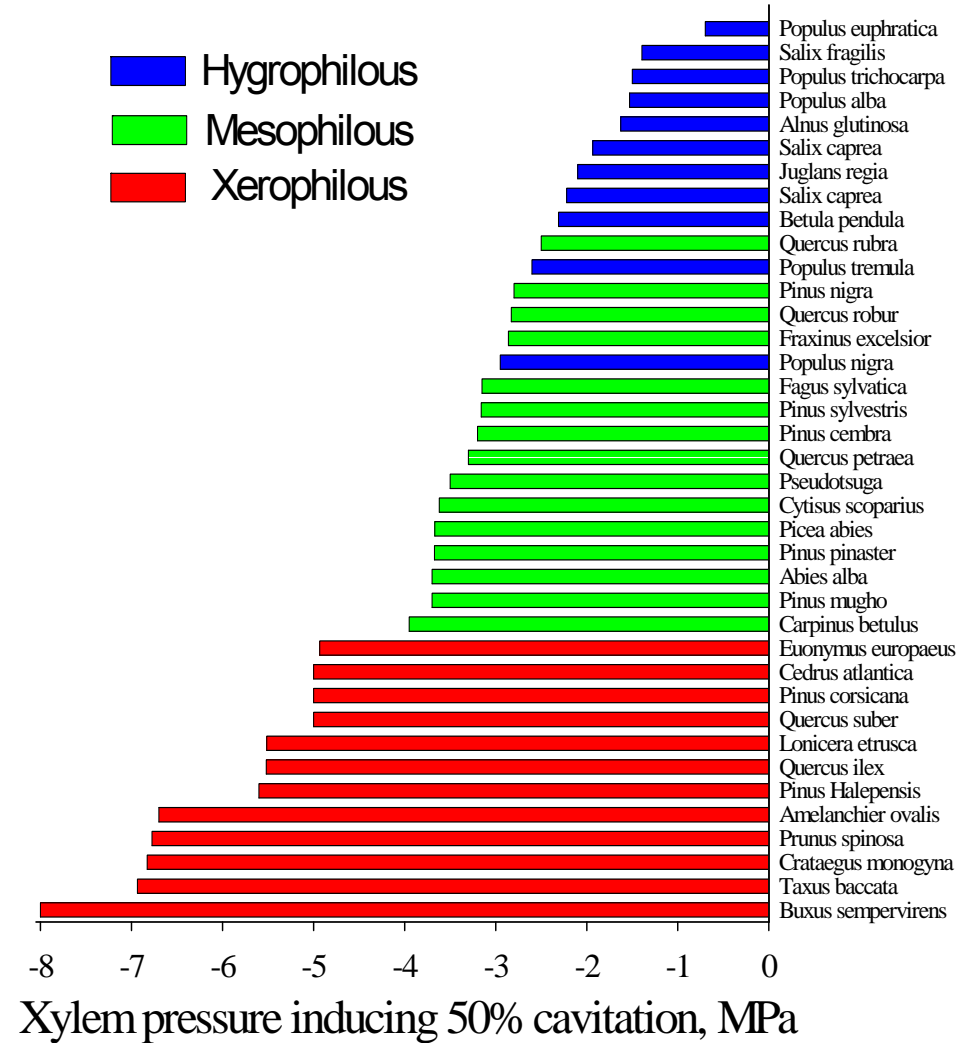
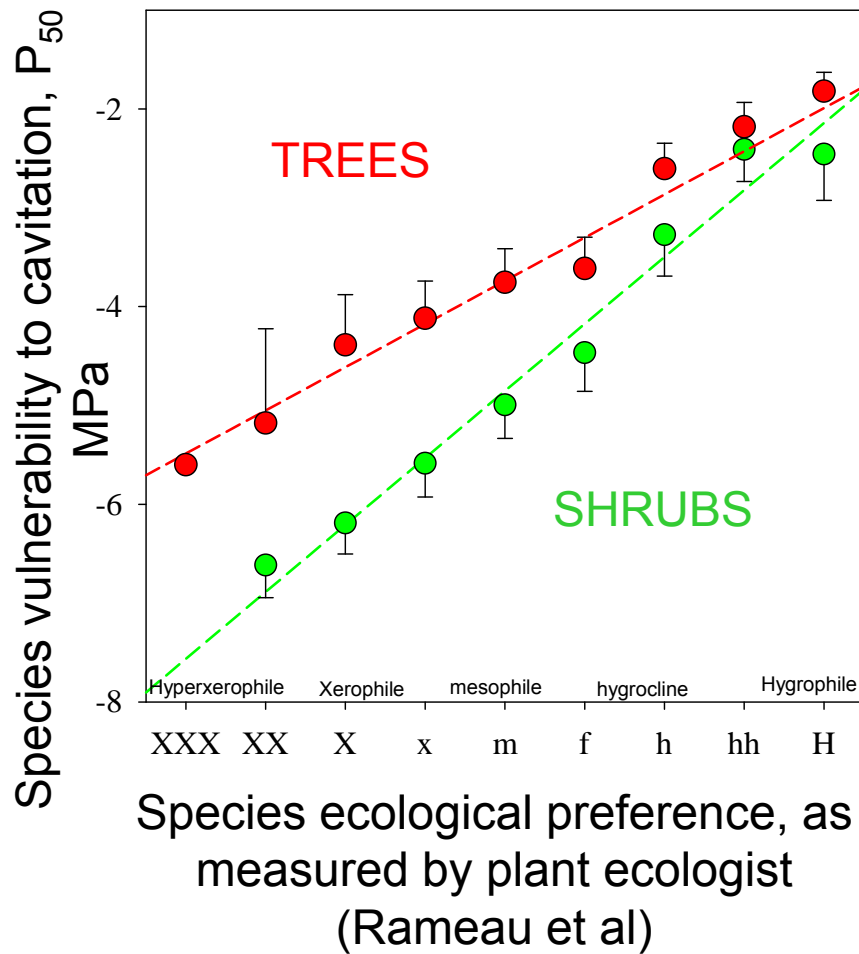
Cavitation resistance (P_{50})

Cavitation resistance correlates with species drought resilience/survival



cavitation resistance seems a good criterion for screening drought tolerance

Cavitation resistance correlates with species ecological preferences



Cochard et al, unpublished

Cavitation resistance versus vegetation type

Vulnérabilité du système conducteur à l'embolie liée à la sécheresse : Ψ_{50}

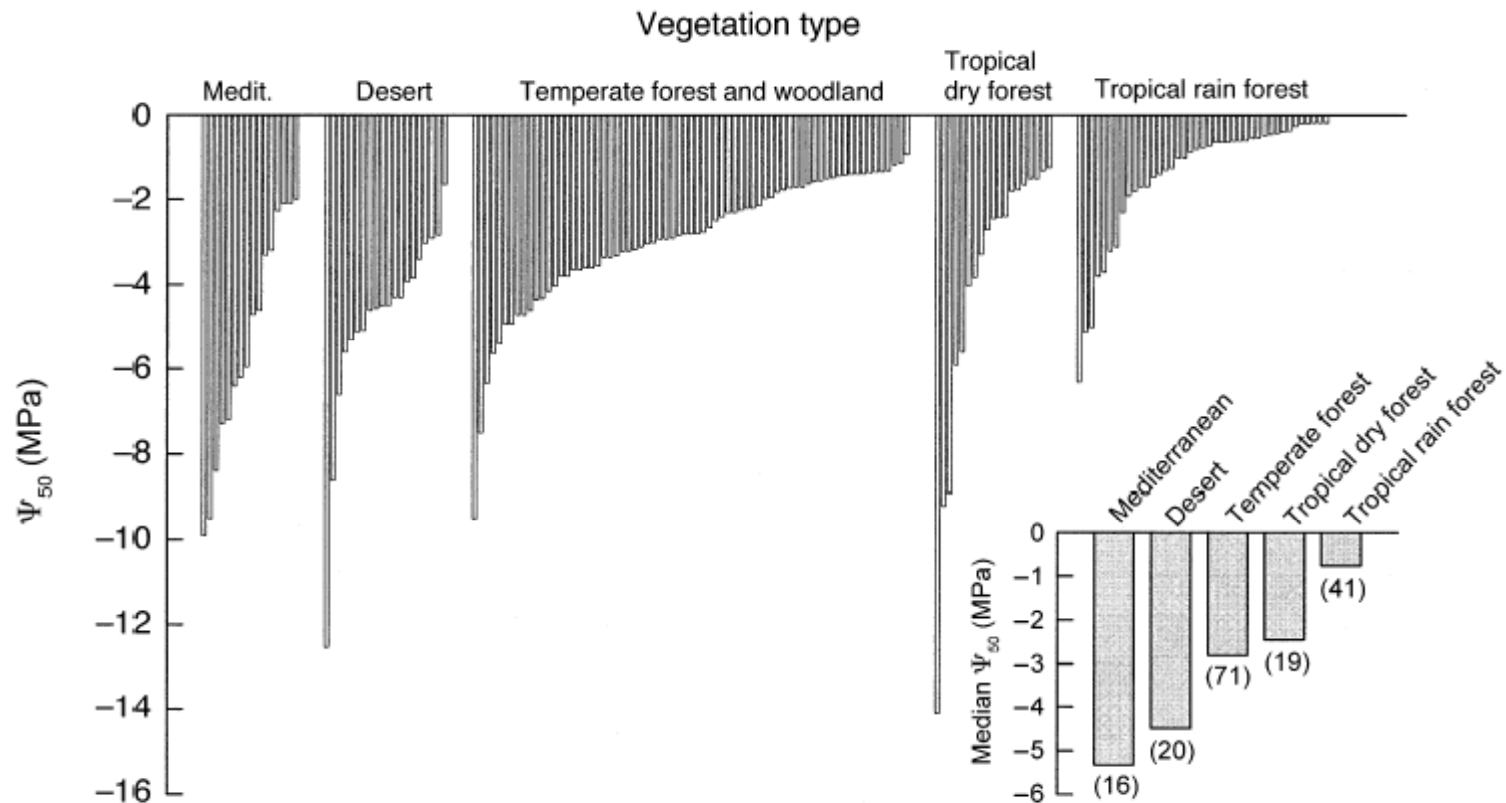


FIG. 1. The distribution of vulnerability to water-stress-induced cavitation (as determined by xylem tension at which 50% cavitation occurred [Ψ_{50}]) for the species used in this database, ranked by magnitude within five vegetation types. The median Ψ_{50} for each vegetation type, along with the sample size for that group, is shown in the inset.



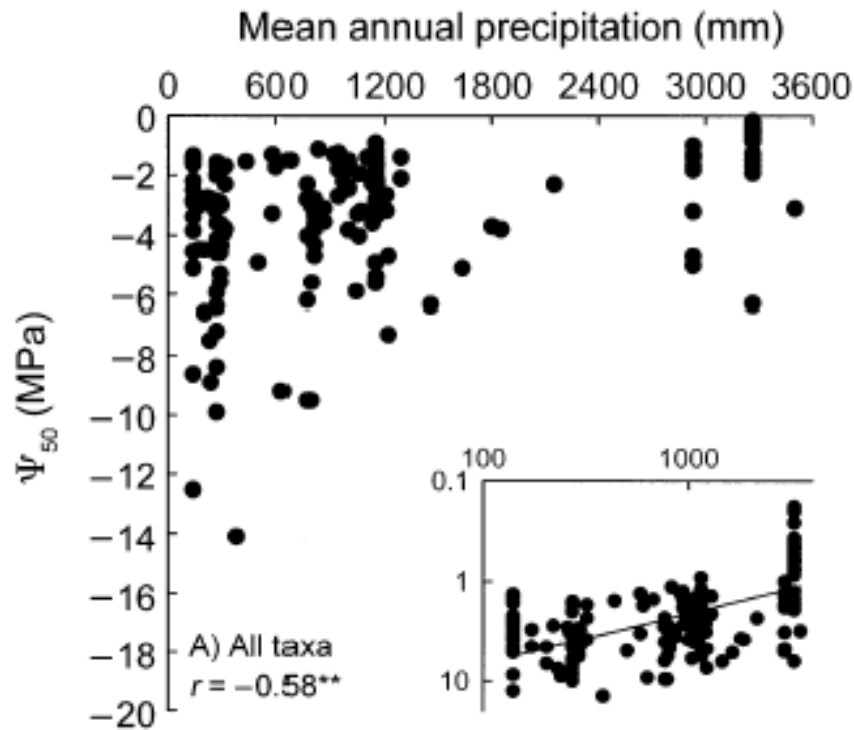
Implications

inter-specific level

A relatively large number of species can now be screened.

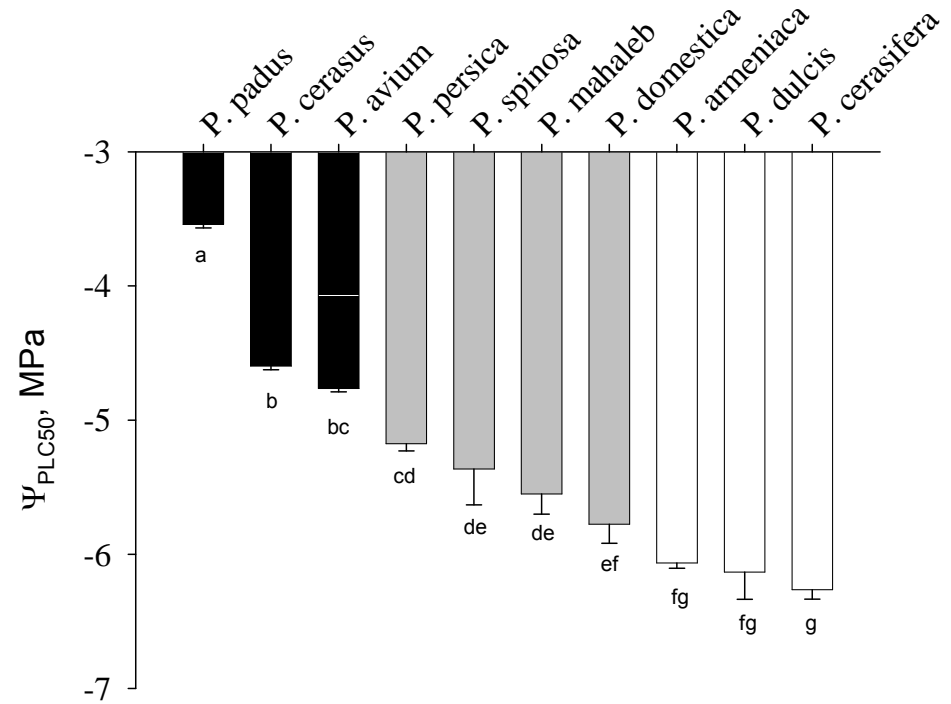
162 species

(angiosperms and gymnosperms)



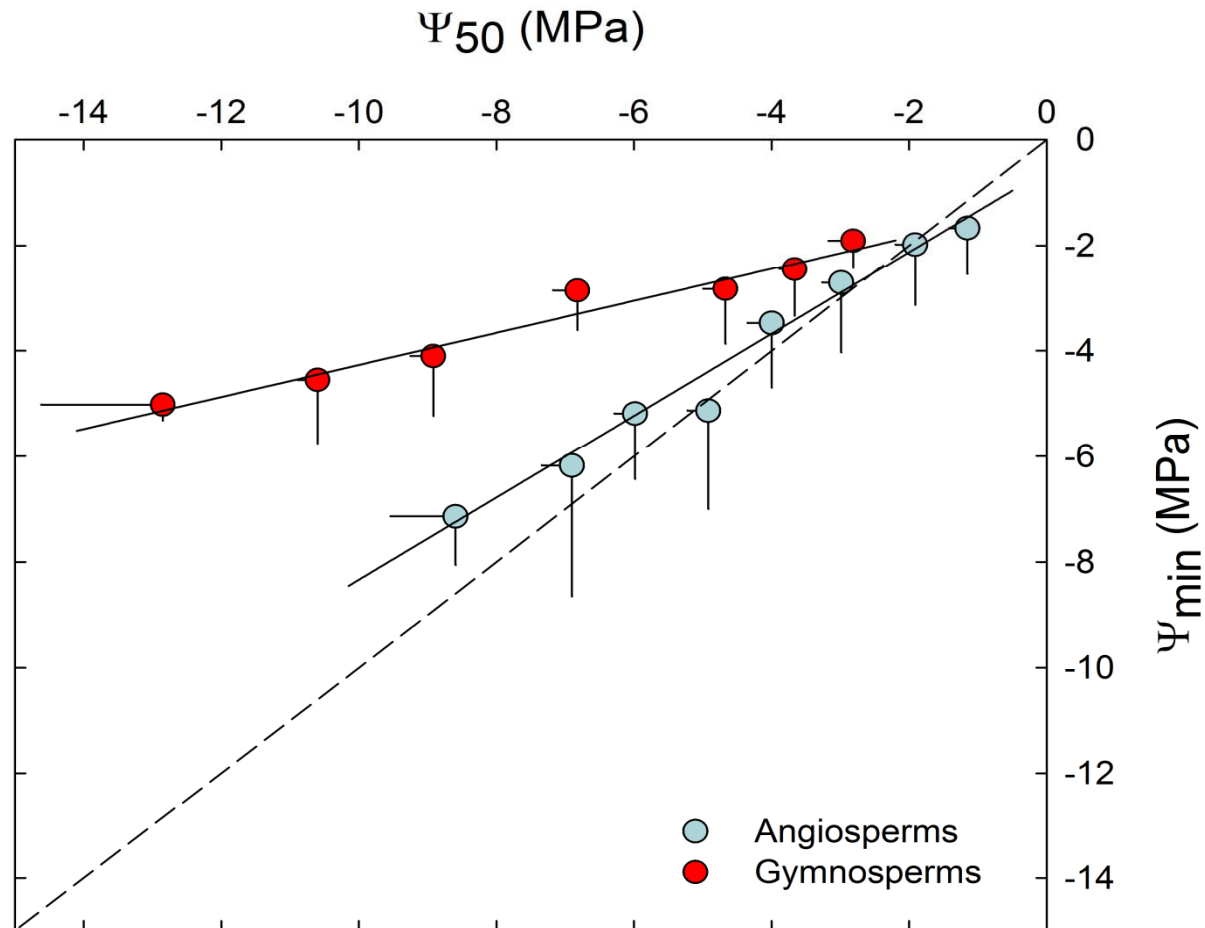
Maherali et al 2004 Ecology

10 species within the genus Prunus

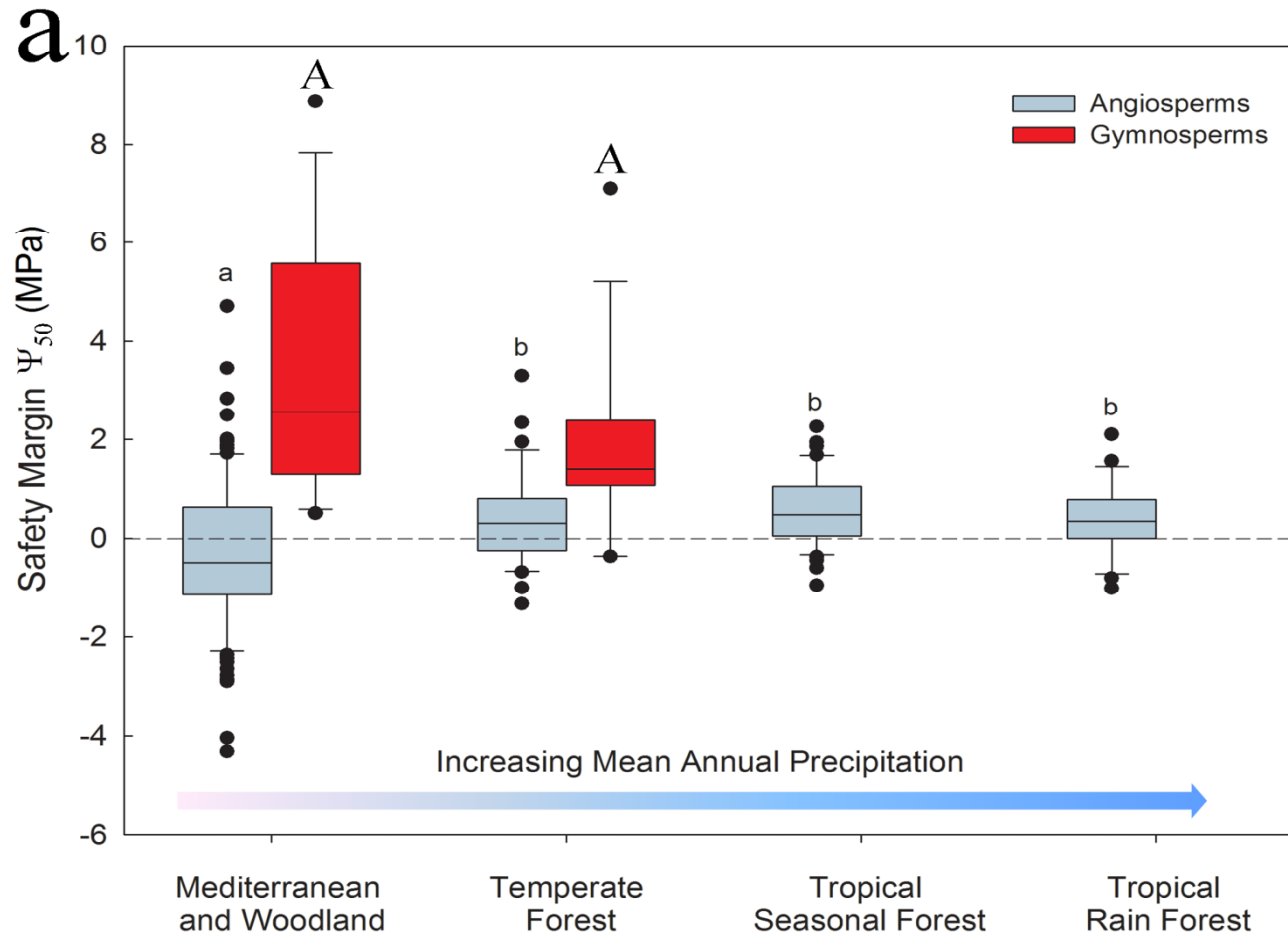


Cochard et al submitted to Plant Cell Environment

Minimum xylem pressure (Ψ_{\min}) as a function of embolism resistance (Ψ_{50}) for 191 angiosperm and 32 gymnosperm species. The dashed line indicates the 1:1 line. The safety margin is the distance between each point and this line. Points were binned in 1.0 MPa increments for Ψ_{50} .



Box plot of hydraulic safety margins for angiosperm and gymnosperm species across major forest biomes. The Ψ_{50} ($\Psi_{\min} - \Psi_{50}$) safety margin is shown in Fig. 2a



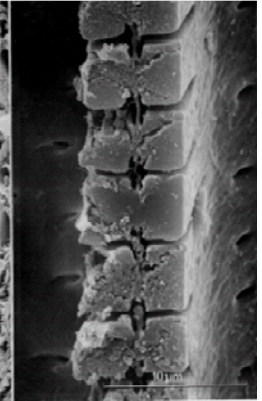
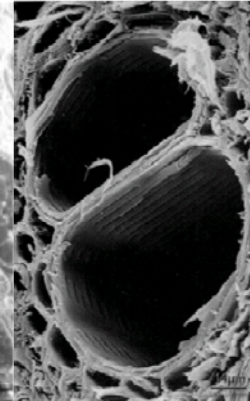
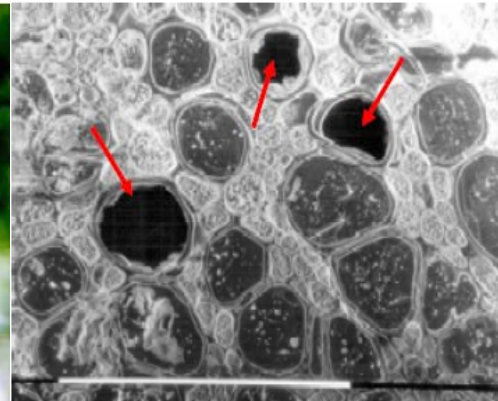
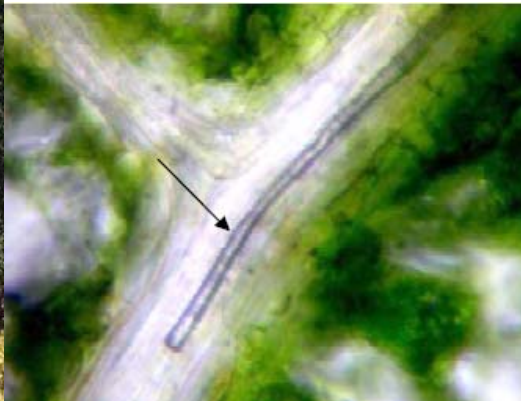
B i o G e C o



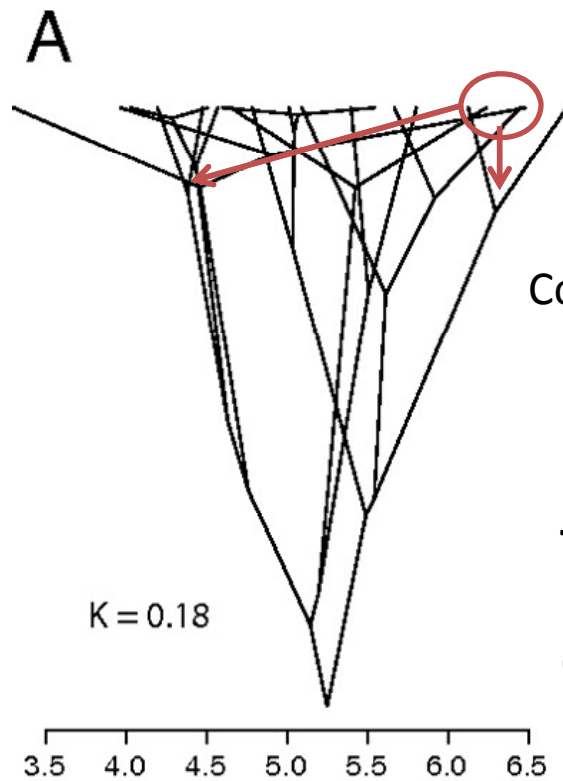
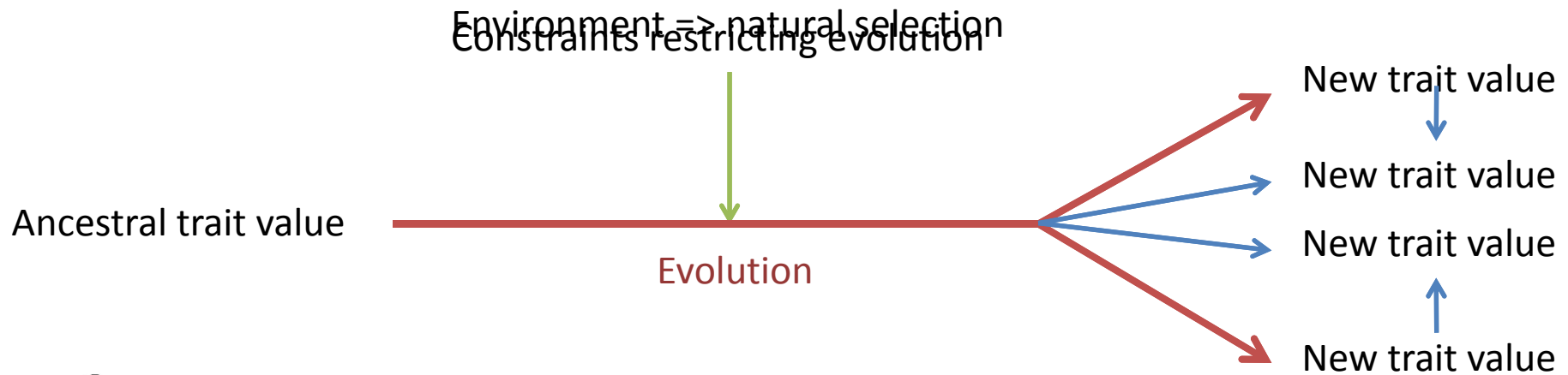
Biodiversité, gènes & communautés



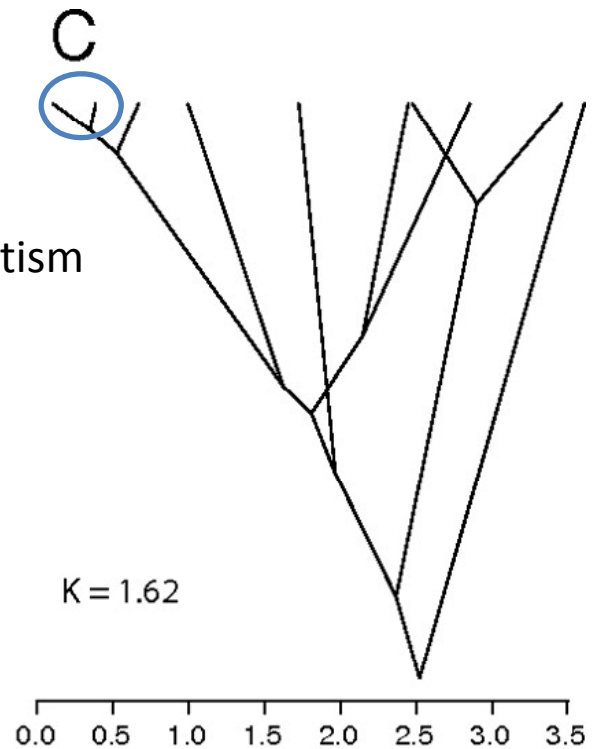
Story III. Evolutionary convergence vs. evolutionary conservatism



Theory: Evolutionary patterns: convergence and conservatism



Traitgrams: species position modified to describe trait values (in this case leaf size)



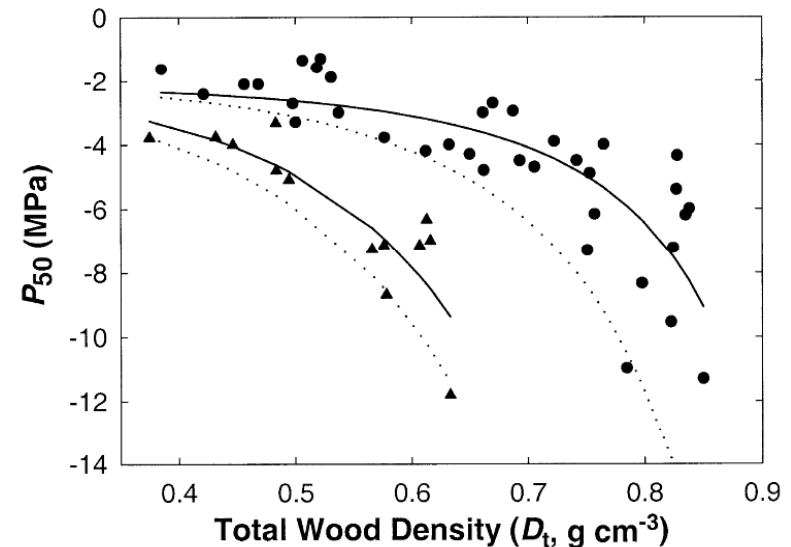
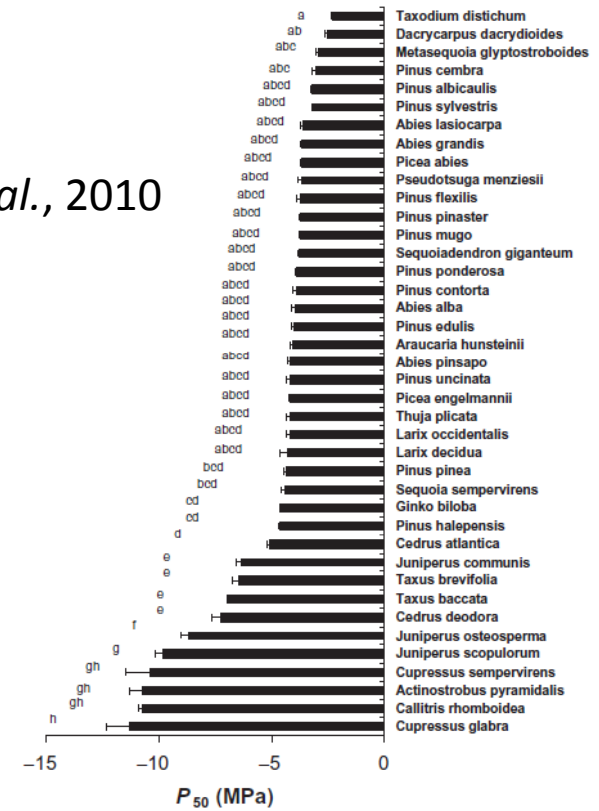
Ackerly, PNAS, 2009

Questions

1. Evolutionary convergence or trait conservatism ?

2. Evolutionary correlations among traits ?

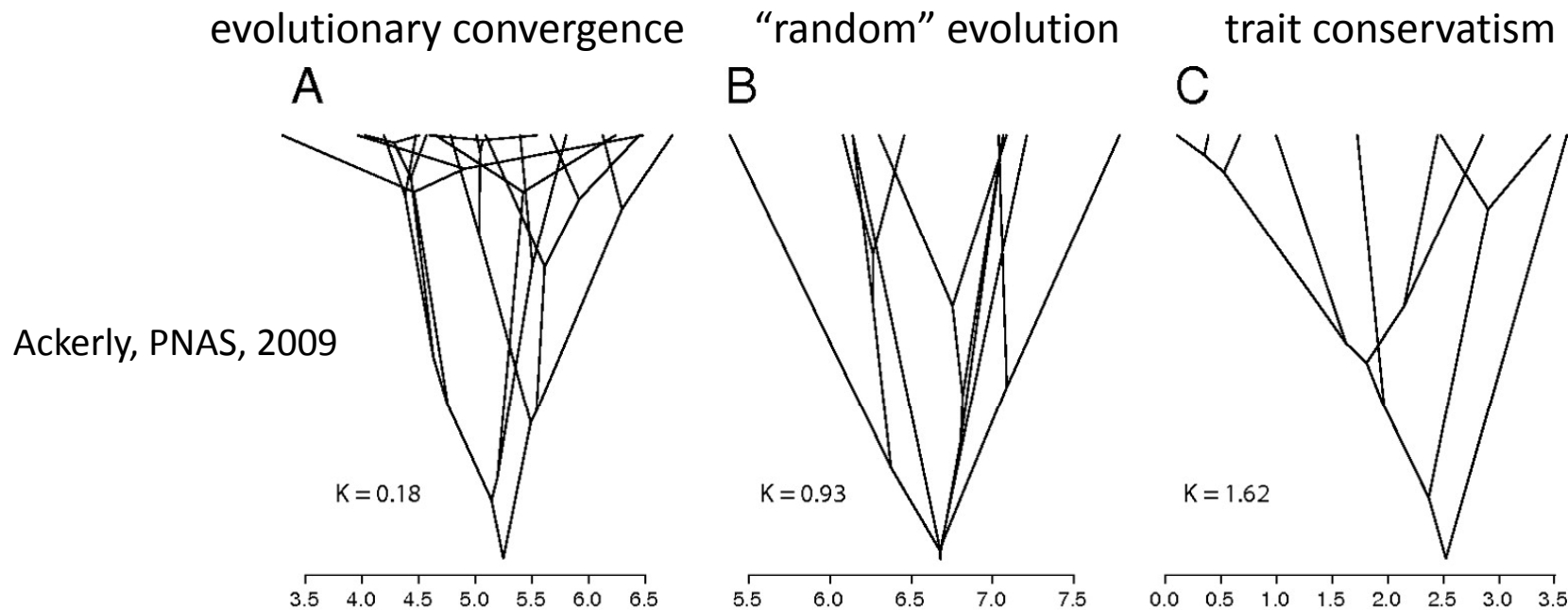
Delzon *et al.*, 2010



Hacke *et al.*, 2001

Methods

- Construction of phylogenetic trees using online sequence database Genbank (genes *rbcl*, *matK*, and *18S*)
- Testing for convergence or conservatism in the data: K (Blomberg, 2003) and λ (Pagel, 1999)

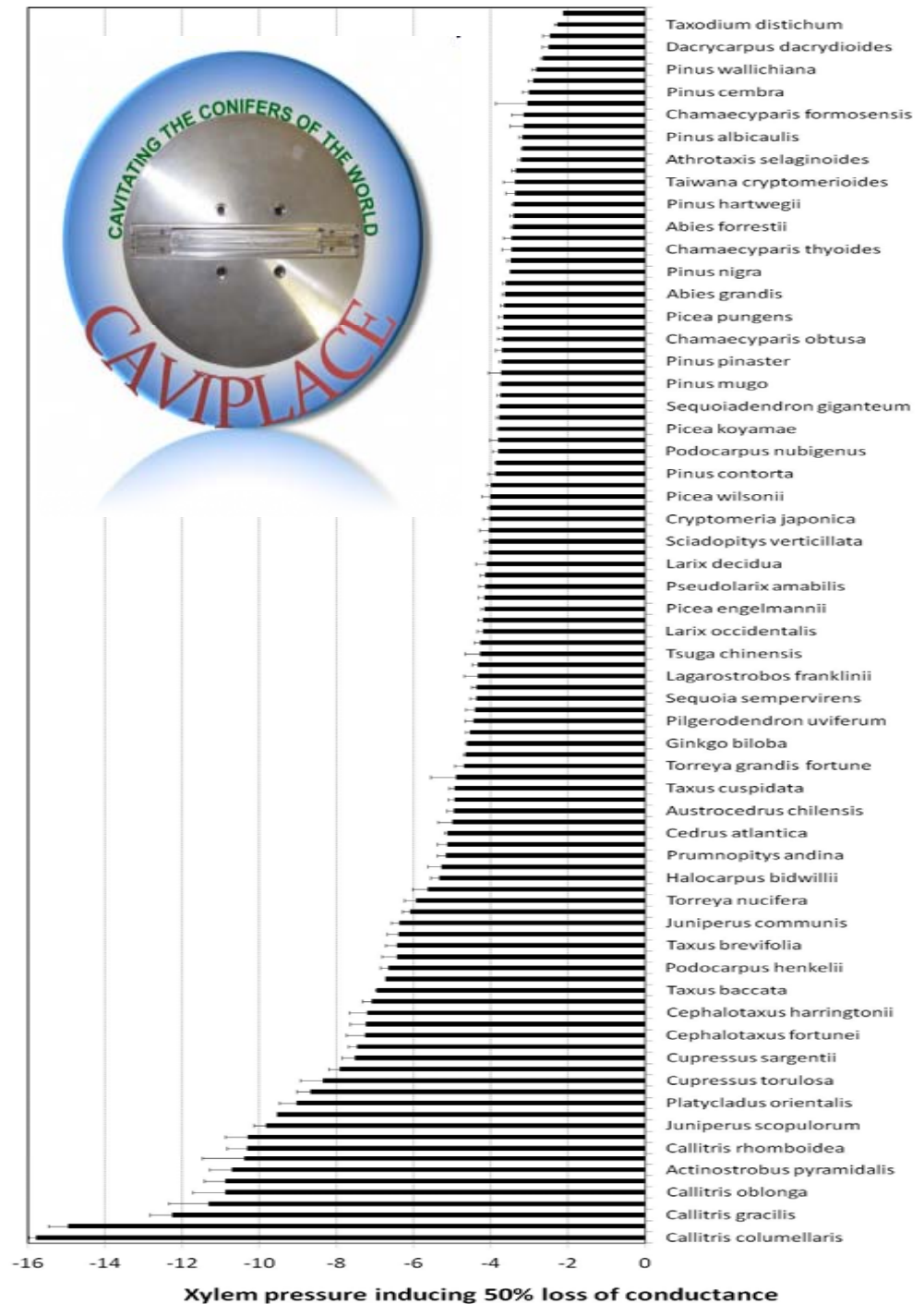


- Correlations and Phylogenetic Independent Contrasts

The worldwide drought tolerance spectrum

Cavitation resistance of 110 conifer species

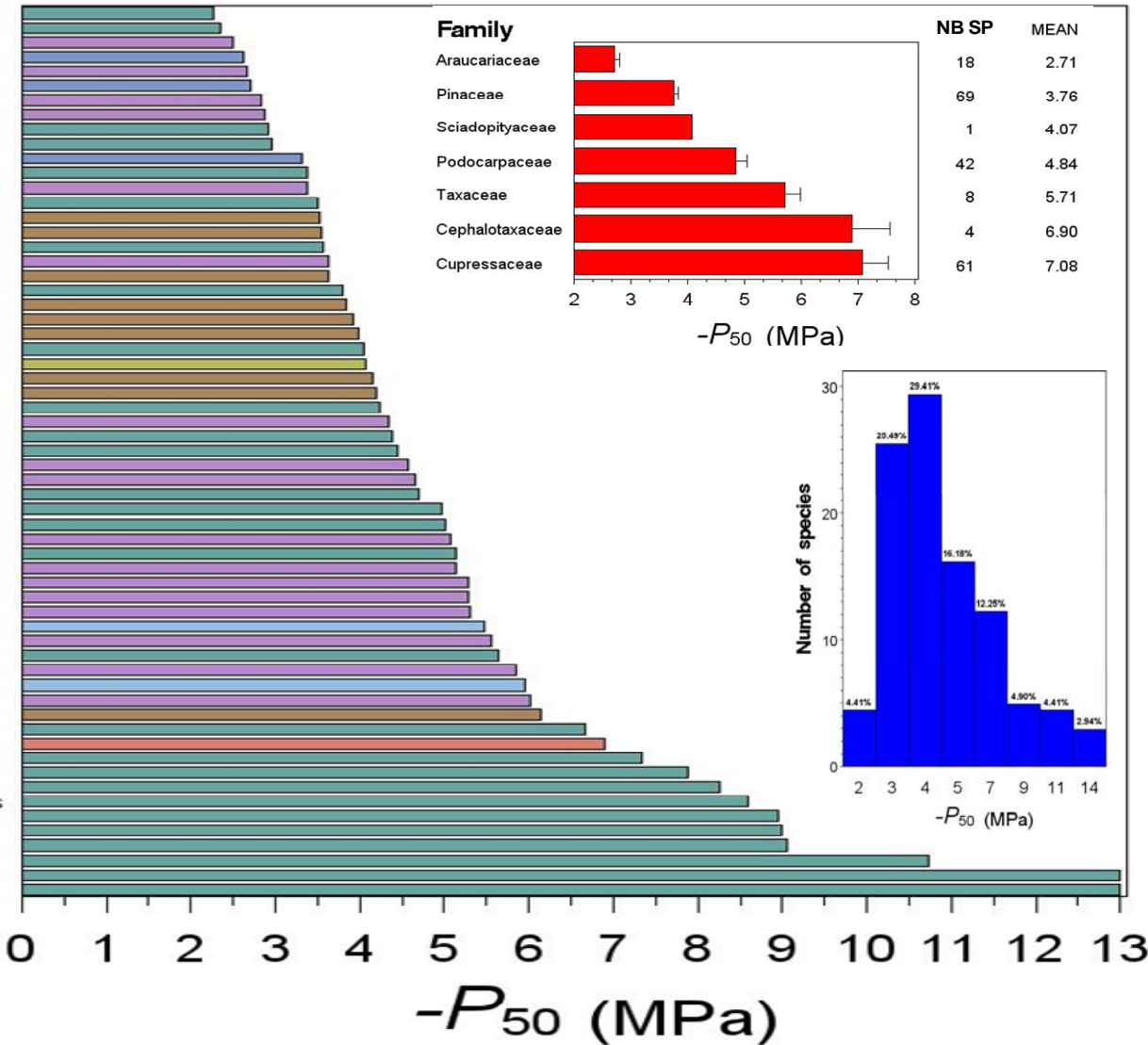
High variability of P50
 from -2.1 (*Agathis australis*)
 to -16 MPa (*Callitris collu*)



3. Cavitation resistance of 60 genera (200 species)

Genus

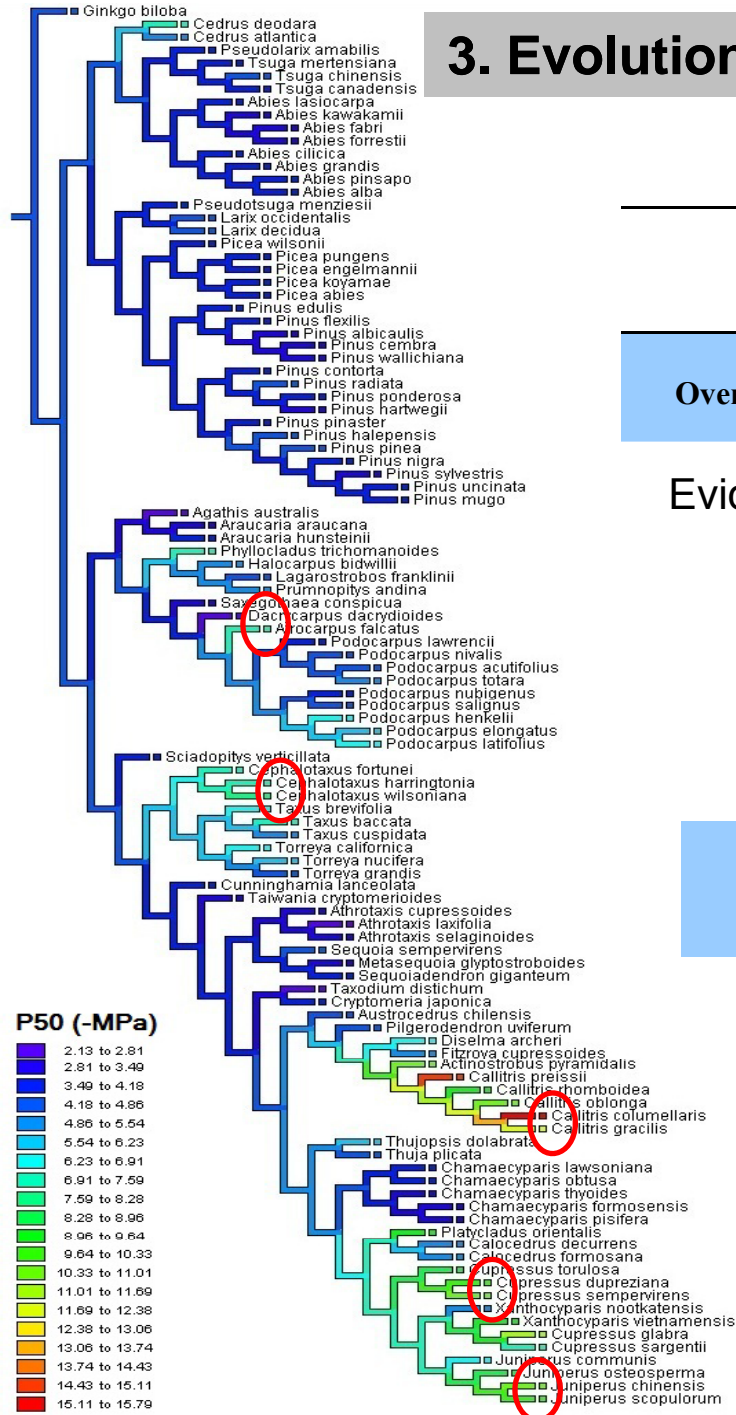
Taxodium
Glyptostrobus
Retrophyllum
Agathis
Dacrycarpus
Araucaria
Sundocarpus
Manoao
Metasequoia
Athrotaxis
Wollemia
Taiwana
Saxegothaea
Cunninghamia
Pinus
Larix
Chamaecyparis
Acmopyle
Abies
Sequoiadendron
Tsuga
Picea
Keteleeria
Cryptomeria
Sciadopitys
Pseudolarix
Pseudotsuga
Thuja
Lagarostrobos
Sequoia
Pilgerodendron
Dacrydium
Nageia
Papuacedrus
Austrocedrus
Fitzroya
Halocarpus
Calocedrus
Pherosphaera
Podocarpus
Microcachrys
Prumnopitys
Torreya
Falcatifolium
Thujopsis
Phyllocladus
Taxus
Afrocarpus
Cedrus
Libocedrus
Cephalotaxus
Xanthocyparis
Widdringtonia
Diselma
Cupressocyparis
Juniperus
Cupressus
Platycladus
Actinostrobus
Tetraclinis
Callitris



High variability of P50
from -2.1 (*Agathis australis*)
to -16 MPa (*Callitris columellaris*)



3. Evolutionary conservatism vs. convergent evolution



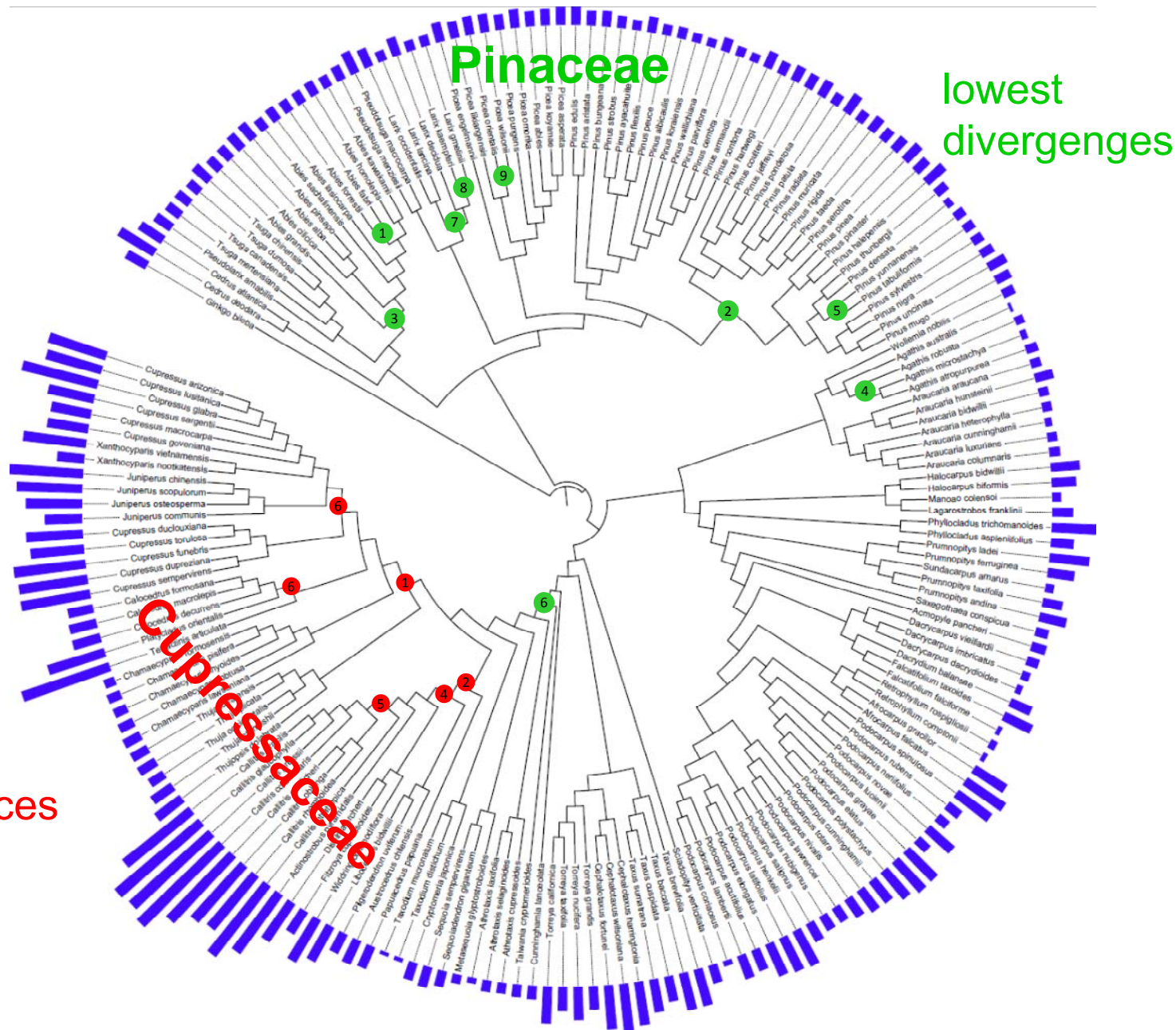
		Blomberg's K values	Pagel's λ values
			(p-value vs. 0 ; p-value vs. 1)
Overall	Index	0.73	0.93
	p	0.001	<0.001 ; 0.041

Evidenced by higher variation in this trait than expected under a Brownian evolution model

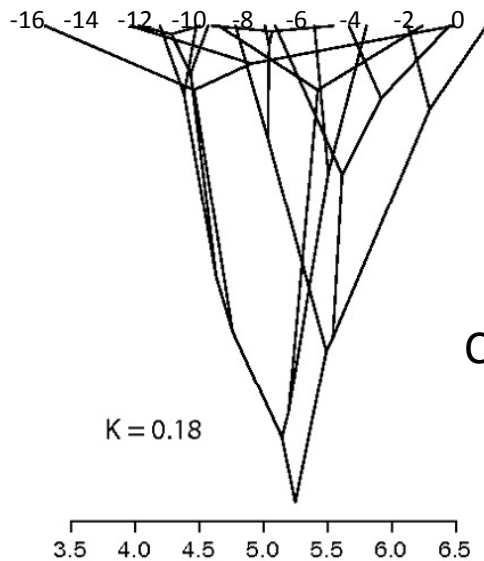
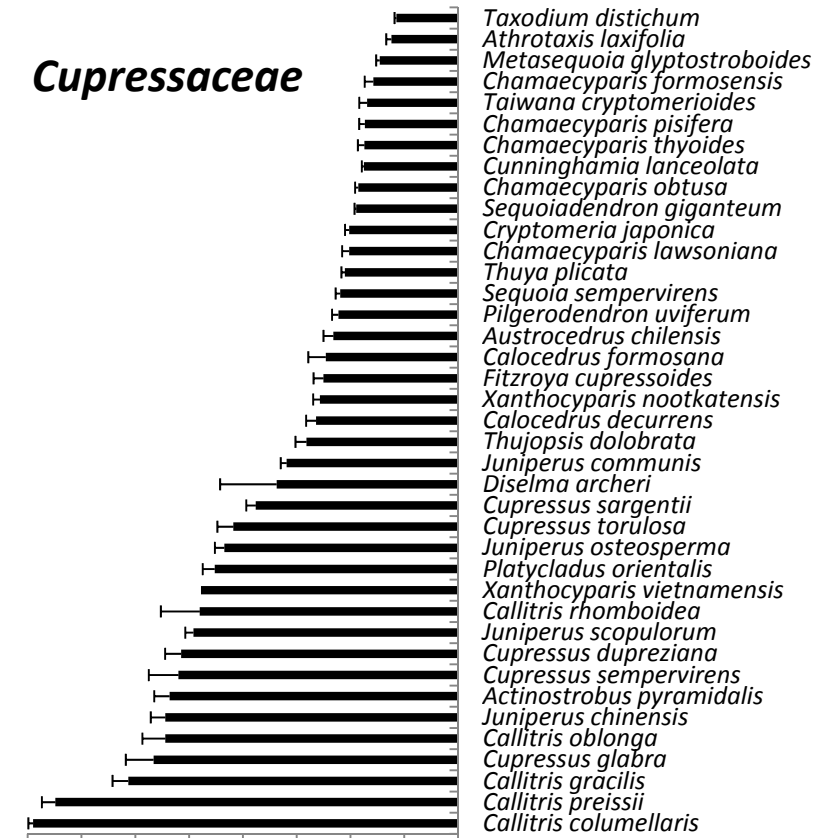
Convergent evolution

The phylogenetic structure of P_{50} values revealed that high resistance to cavitation appeared several times.

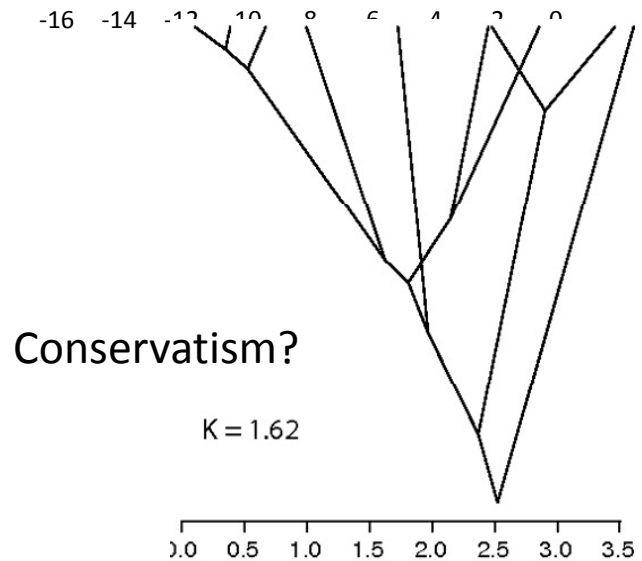
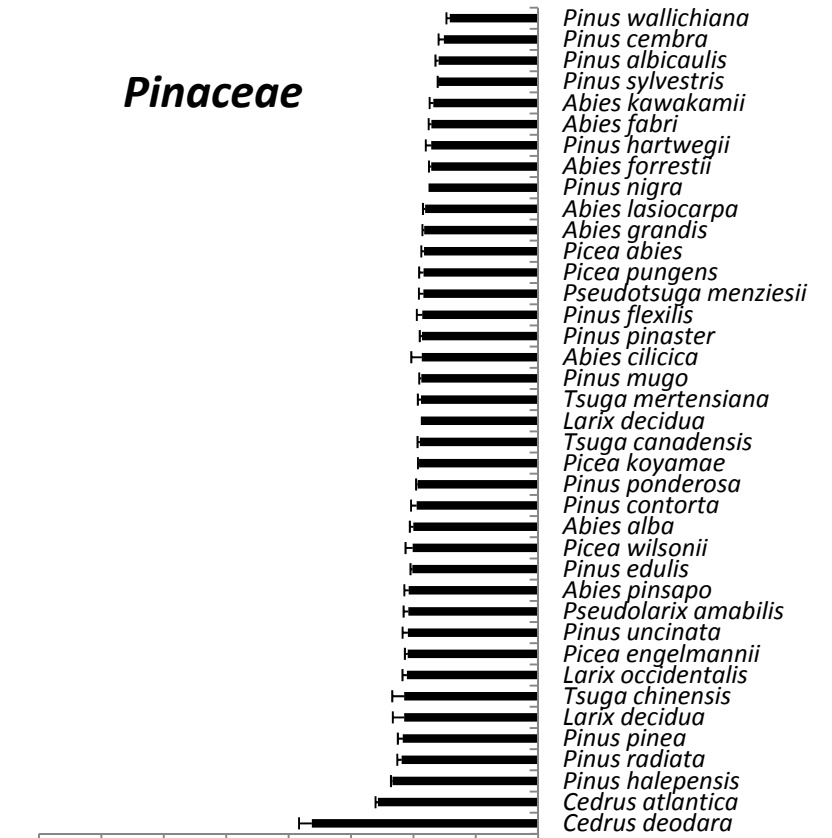
3. Different families, different evolutionary histories



Cupressaceae

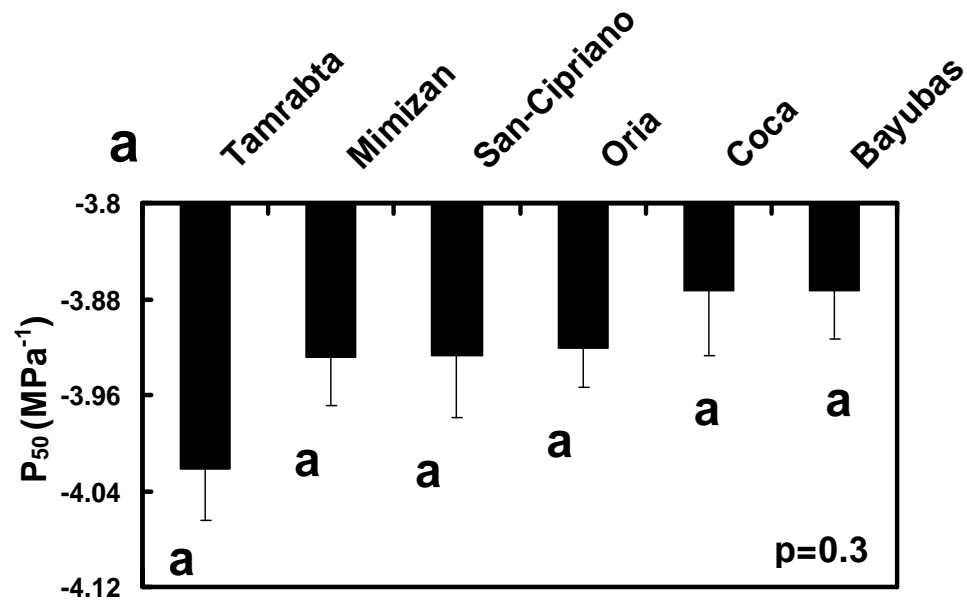


Pinaceae



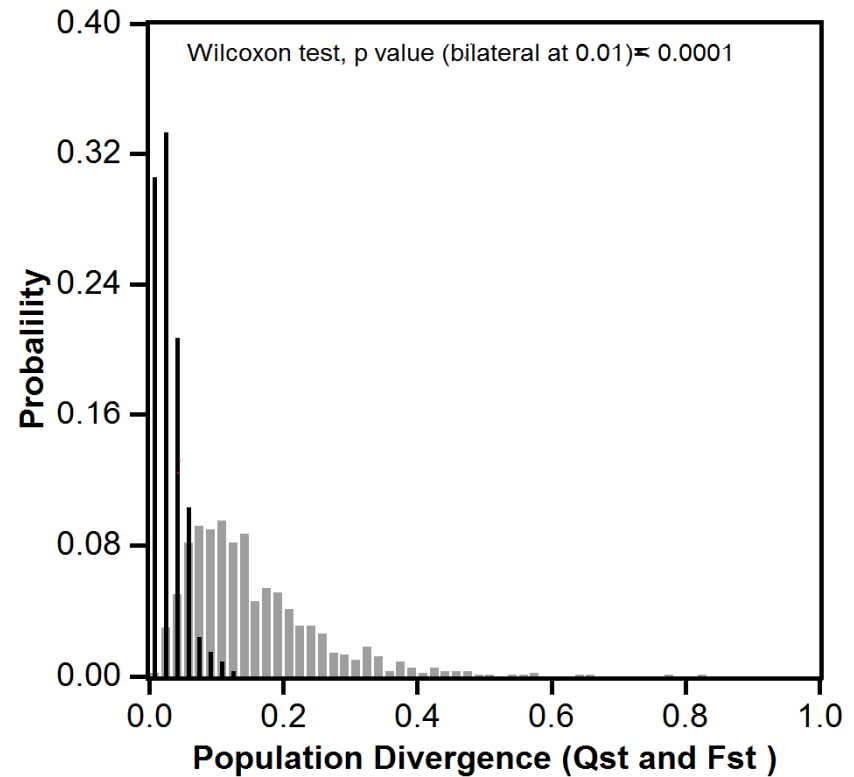
4. Intra-specific (*Pinus pinaster*)

Lack of genetic variation in cavitation resistance among populations across a species distribution range



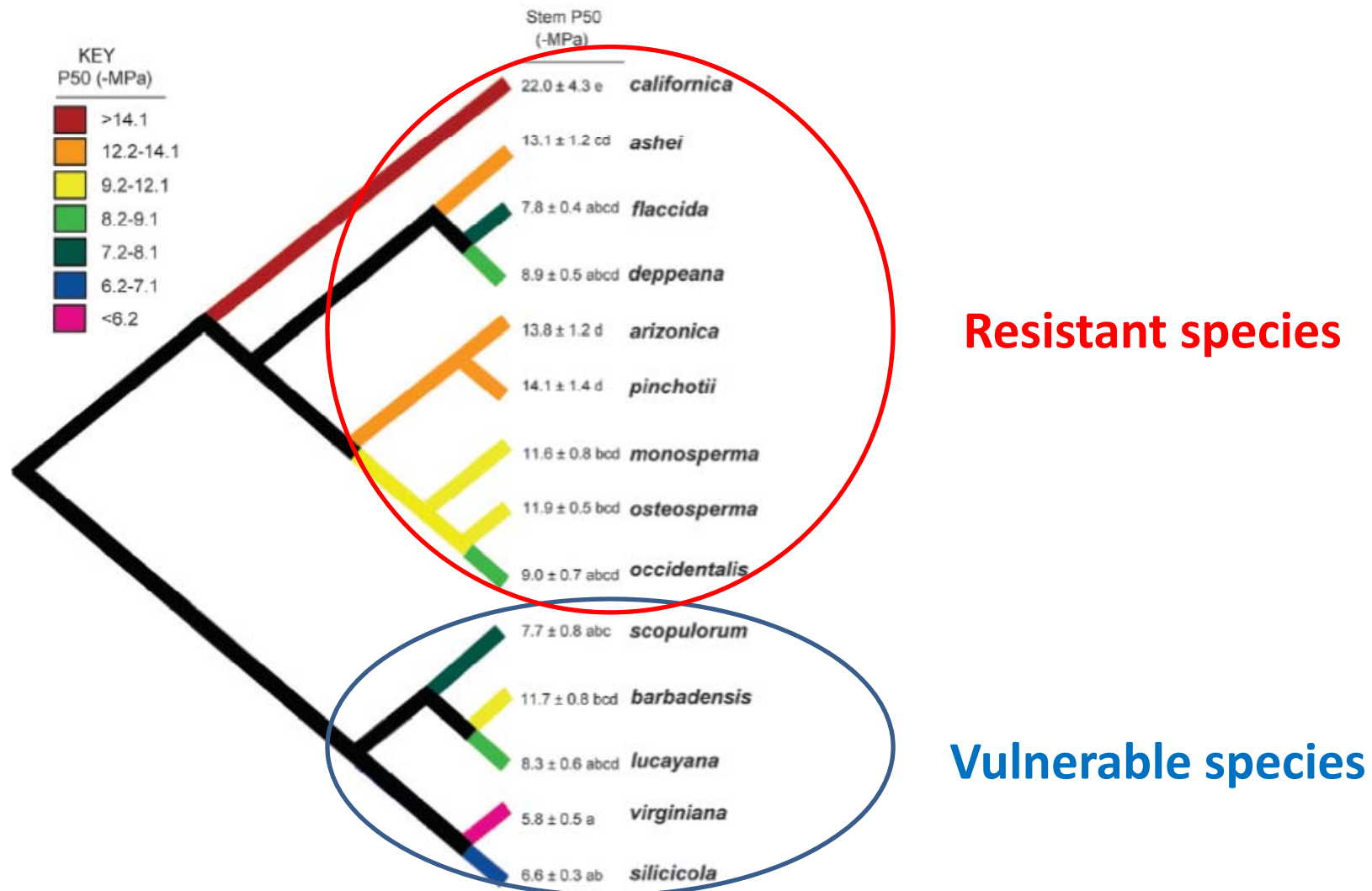
The $Q_{ST} < F_{ST}$ pattern can be interpreted as a canalization phenomenon or a consequence of uniform selection

Qst and Fst distribution of P50

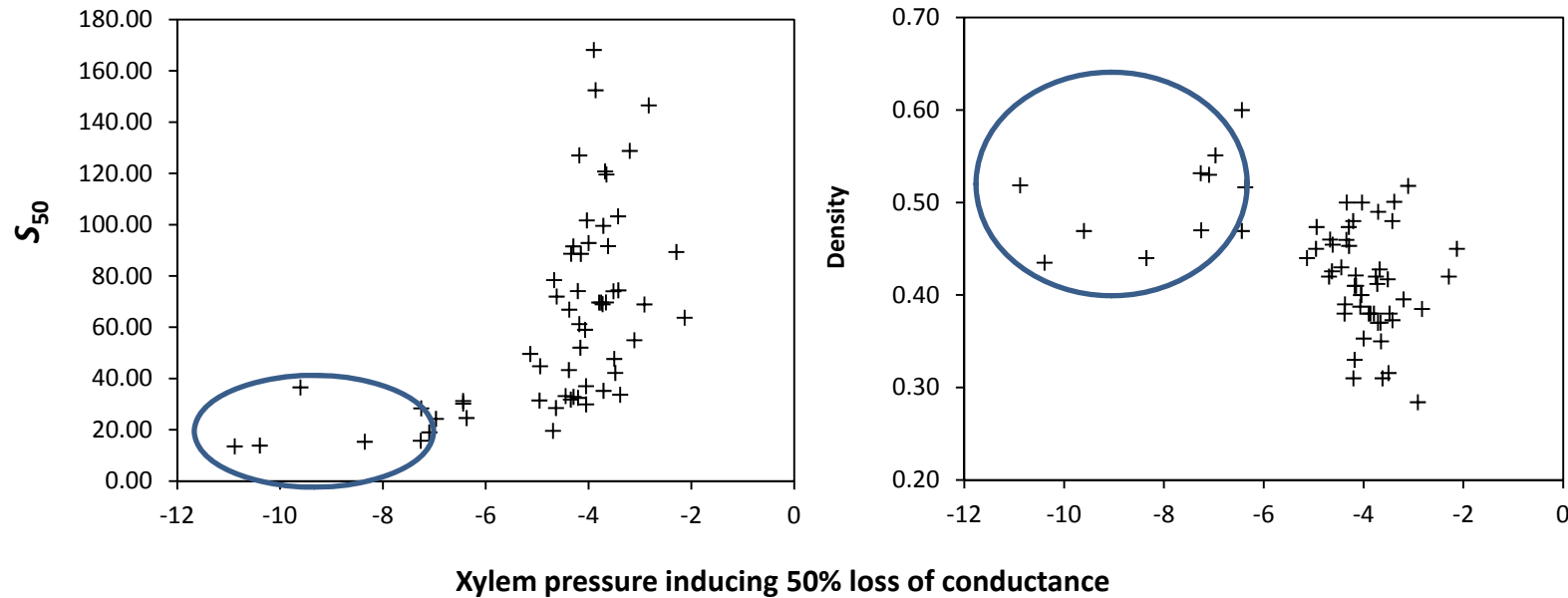


Previous studies:

- Willson et al. (2008): genus *Juniperus* (North America):
=> Trait conservatism



Trait correlations and PICs



	r	P	PIC	P
Correlation with P_{50}				
Density	0.47	<0.001	0.27	0.046
S_{50}	-0.55	<0.001	0.34	0.012

Resistant species cavitate later and slower than vulnerable species
 Resistance to cavitation and wood density show correlated evolution
 Wood density is higher for resistant species

Etude de cas: coexistence de trois espèces / stratégies hydriques

Pin d'Alep :

Pionnière
(propagation par graine)
Futaie, pas de tradition de gestion
Elle est considérée
comme peu exigeante



Chêne vert :

Traité traditionnellement en taillis
(régénération par rejets de souche)
Résistant à la contrainte hydrique



Buis :

Longévive. Croissance lente
(marcottage naturel)
Pas ou peu exploité
Résistant à la contrainte hydrique

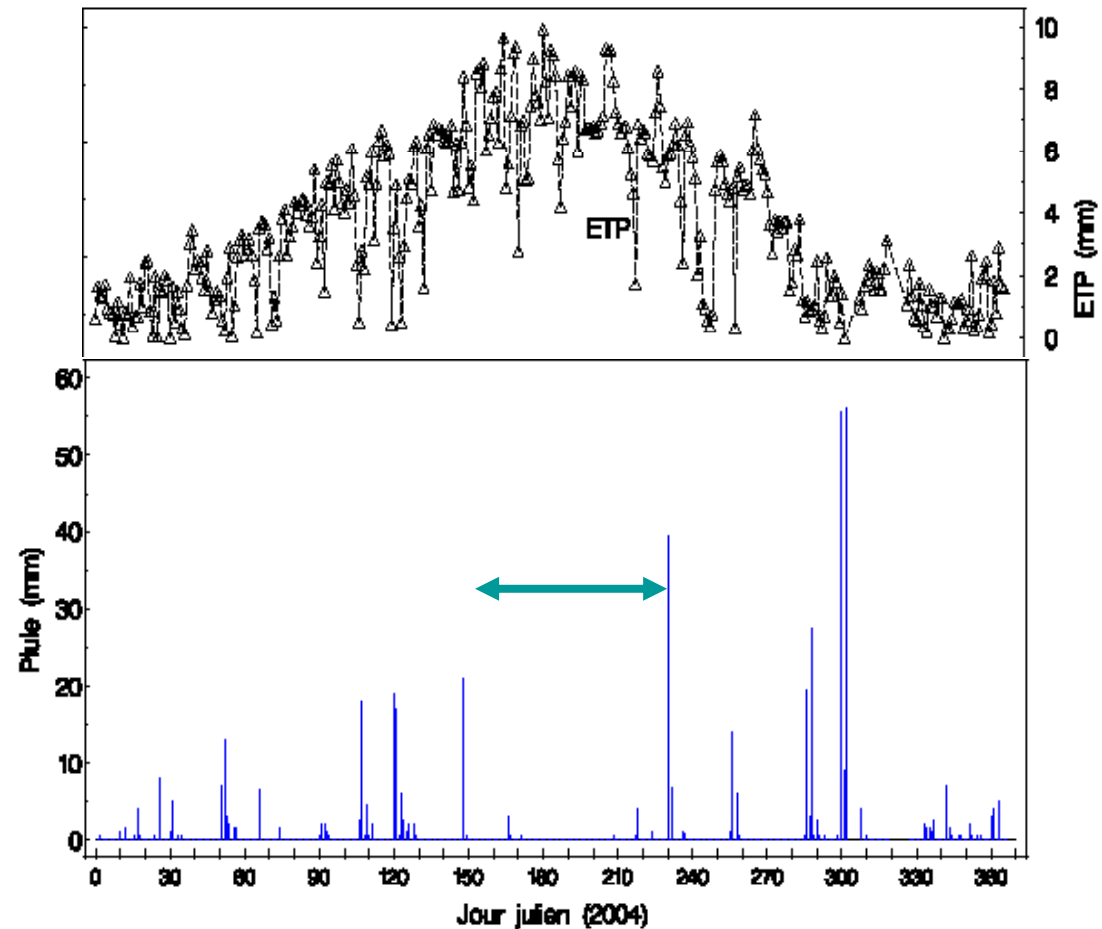
2. Le stress hydrique : exemple sous climat méditerranéen

Milieu méditerranéen :

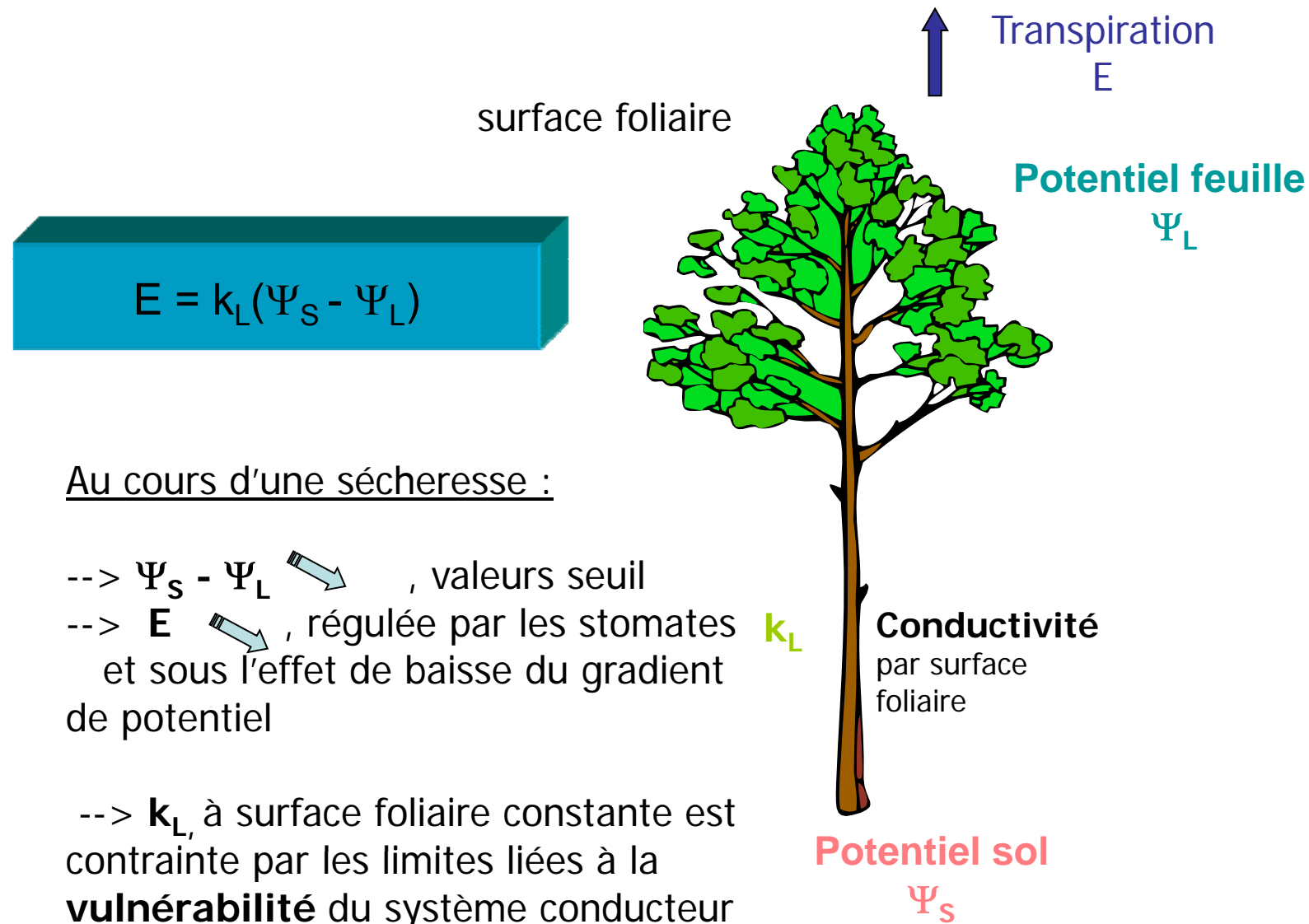
climat à été chaud et sec
sols à fortes contraintes
hydriques

Quelles conséquences sur les
caractéristiques hydrauliques
des espèces ?

Quelles répercussions pour le
fonctionnement ?

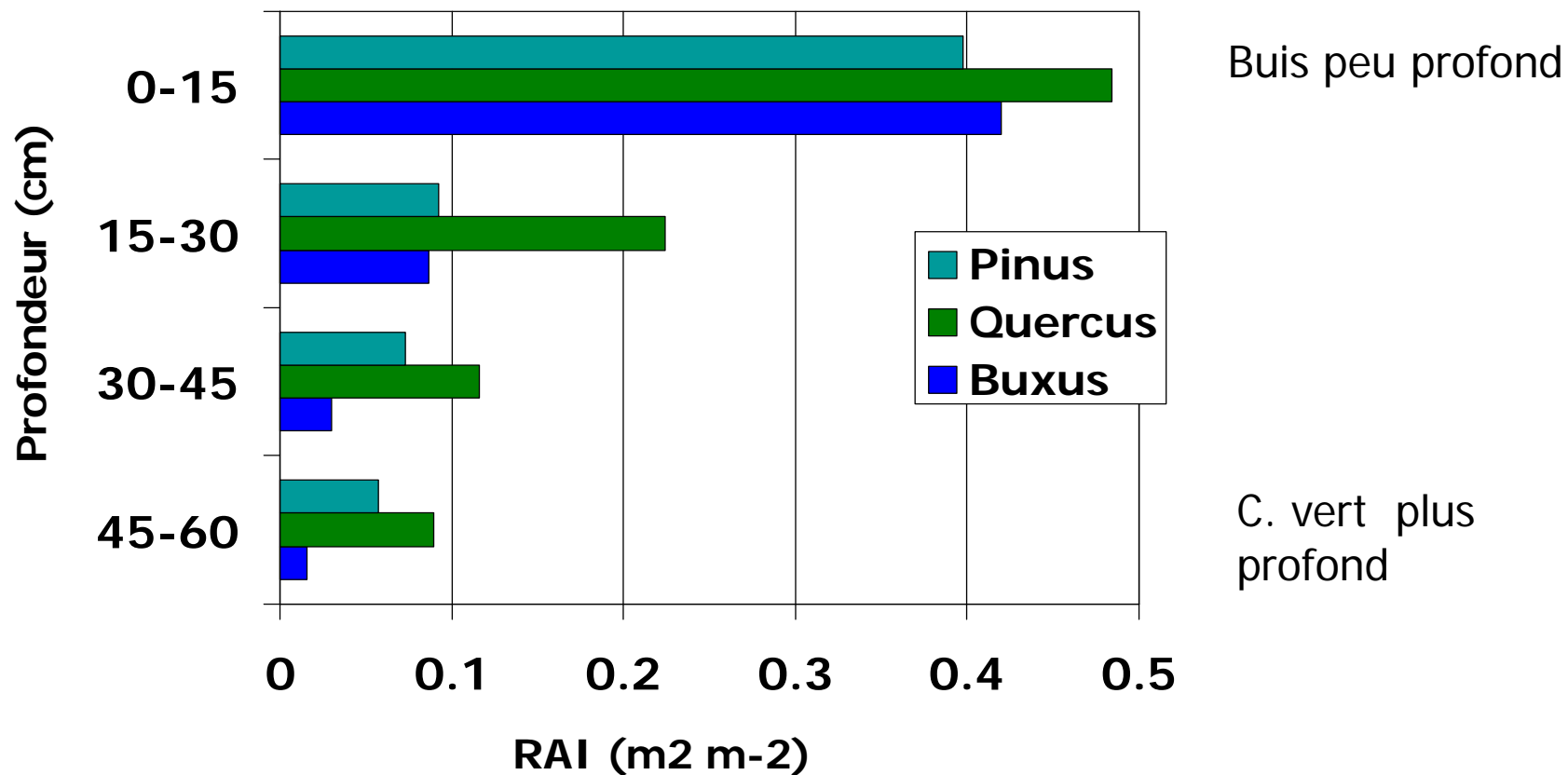


Fonctionnement hydraulique



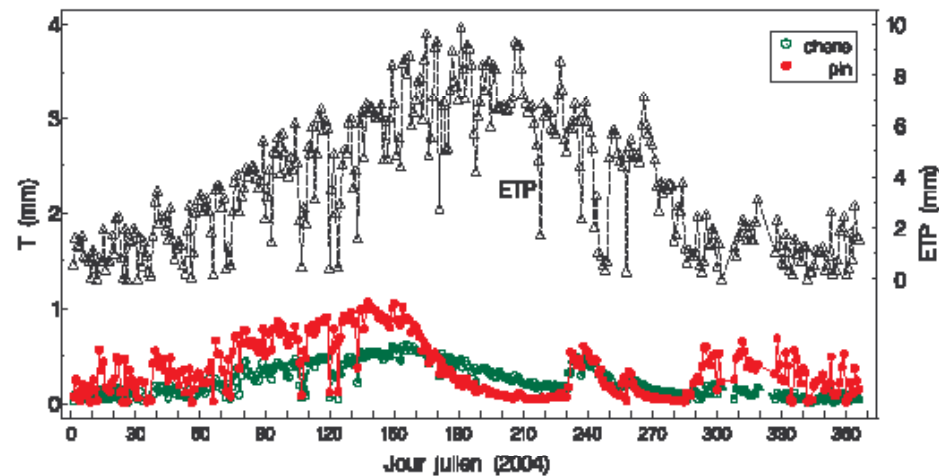
Etude de cas: coexistence de trois espèces / stratégies hydriques

Profils d' Enracinement

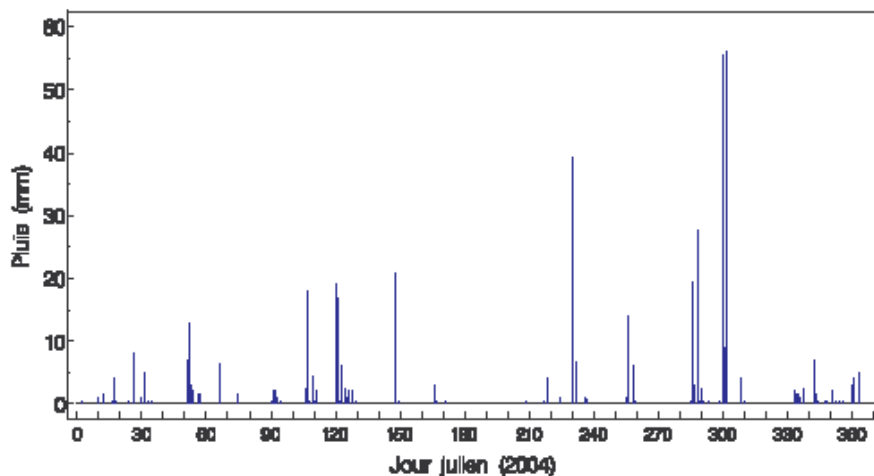


Etude de cas: coexistence de trois espèces / stratégies hydriques

Transpiration chêne et pin

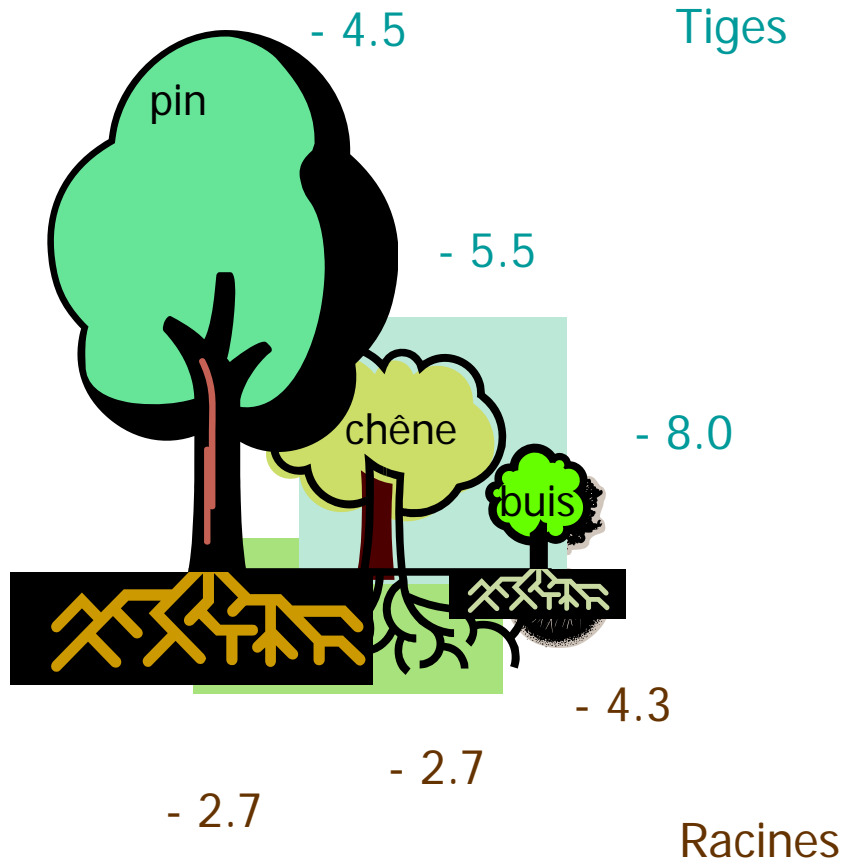


Le pin d'Alep (espèce isohydrique) régule fortement sa transpiration (fermeture stomatique)



Reprise de la transpiration en fin de saison sèche

Etude de cas: coexistence de trois espèces / stratégies hydriques



Vulnérabilité à la cavitation

Vulnérabilité racines > tiges

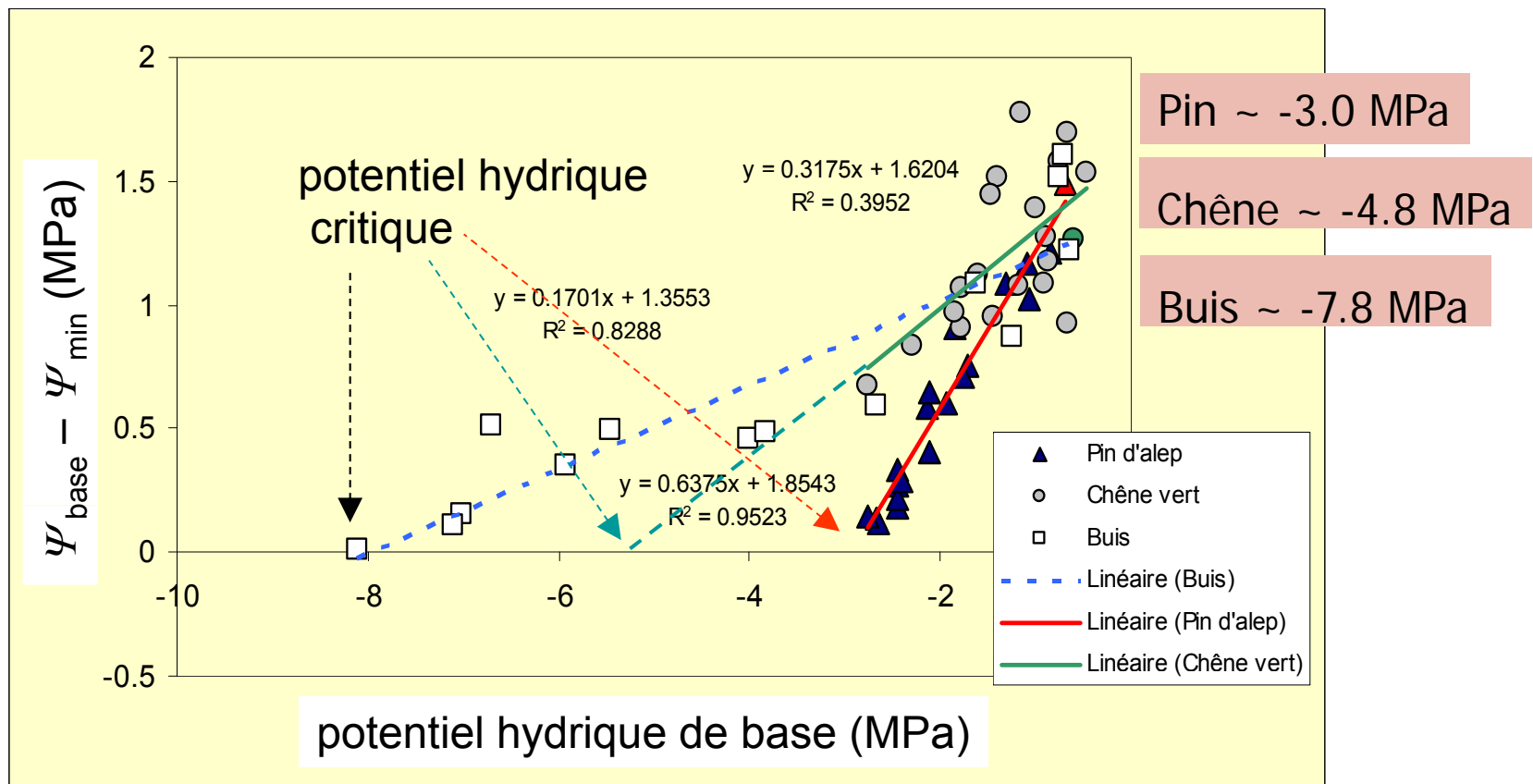
- Tiges
pin d'Alep = Q. ilex > B. sempervirens

- Racines :
pin d'Alep = Q. ilex > buis

Valeurs de potentiel (en MPa) induisant 50 % de perte de conductivité

Etude de cas: coexistence de trois espèces / stratégies hydriques

Seuils de fonctionnement



Etude de cas: conclusions

Importance de la vulnérabilité et comportement des espèces

- Buis système conducteur **très peu vulnérable**, fonctionne sous très fort stress (**tolerance**)
- Chêne, **vulnérable**, fonctionne sous fort stress mais possède des capacités d'extraction en profondeur (**avoidance, Water spender**)
- Pin, **très vulnérable**, arrête de fonctionner sous fort stress (**avoidance, Water saver**)