Drought in tropical forests

The role of tree height and wood density for hydraulic efficiency, productivity and vulnerability to cavitation of trees along a lowland precipitation gradient

Roman Link

Department of Plant Ecology and Ecosystem Research
Georg August University of Göttingen

January 25, 2018

Structure of my PhD project

- Introduction
- **Chapter 1:** Predicting radial sap flow profiles from Costa Rican tropical dry forest species
- **Chapter 2:** Estimating plant vulnerability to embolism in Costa Rican humid tropical forest species
- **Chapter 3:** Relationship between productivity, structural and functional, wood anatomical and hydraulic traits of tropical forest species from Costa Rica

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- **Bonus Chapter:** Maximum-likelihood estimation of xylem vessel lengths

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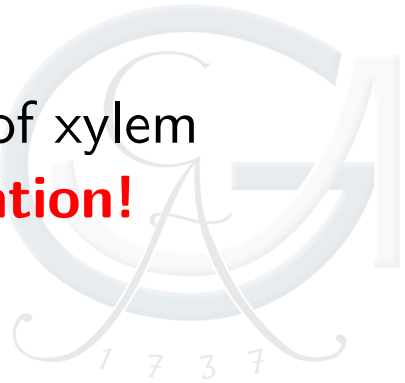
- **Bonus Chapter:** Maximum-likelihood estimation of xylem vessel lengths: **Not in the focus of this presentation!**



Introduction

- Basics about plant water relations
- Why is it important to know about drought effects in the tropics?

Main research questions

- This one's gonna be tough

Design of the study

- 5 research sites along a rainfall gradient on the Pacific shoreline of Costa Rica
- Gradient from tropical dry forest to humid tropical lowland forest
- Based on existing research sites of the **Instituto Tecnológico de Costa Rica**

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At each of the 5 research sites:

- 8 species representing a gradient in tree height and wood density
- 5 replicates per species

$\Rightarrow$ 40 trees per site, 200 trees in total

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- **Variables measured at all sites**
  - Tree level
    - Diameter at breast height
    - Tree height
    - Tree growth (basal area/aboveground biomass increment)
    - Wood density
    - Sapwood non-structural carbohydrate (NSC) content
  - Site level
    - Temperature
    - Relative humidity
    - Precipitation
- **Variables measured at a subset of sites**
  - Sap flow (only at one site)
  - Branch vulnerability to embolism (only at two sites)

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Problems with the design

- Opportunistic use of pre-existing plots
  - Different plot sizes and numbers at each site
  - Differences in historic land use (pristine primary forest vs. disturbed primary forest vs. secondary forest)
  - Cooperation with forestry department (foresters do forester things...)

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$\rightarrow$ Plot-based comparisons are difficult

$\Rightarrow$ Not that important for our (eco-physiological) research questions, but limits usability of plot network for other research areas

First chapter: radial sap flow profiles

Sap flow measurements:

- Practical limitations → only in dry forest (Horizontes)
- 4 measurement campaigns of ± 1 week during rainy season of 2015
- 40 trees of 8 species
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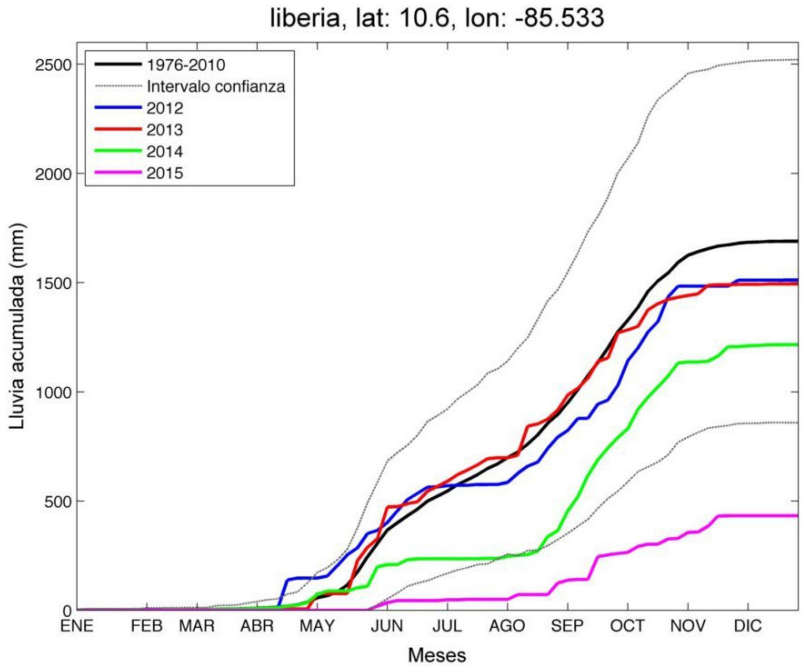

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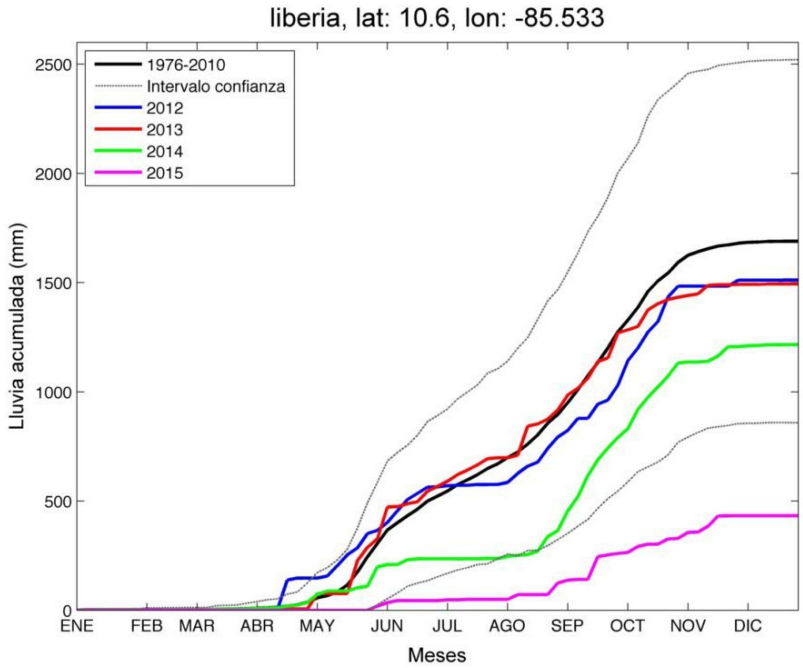

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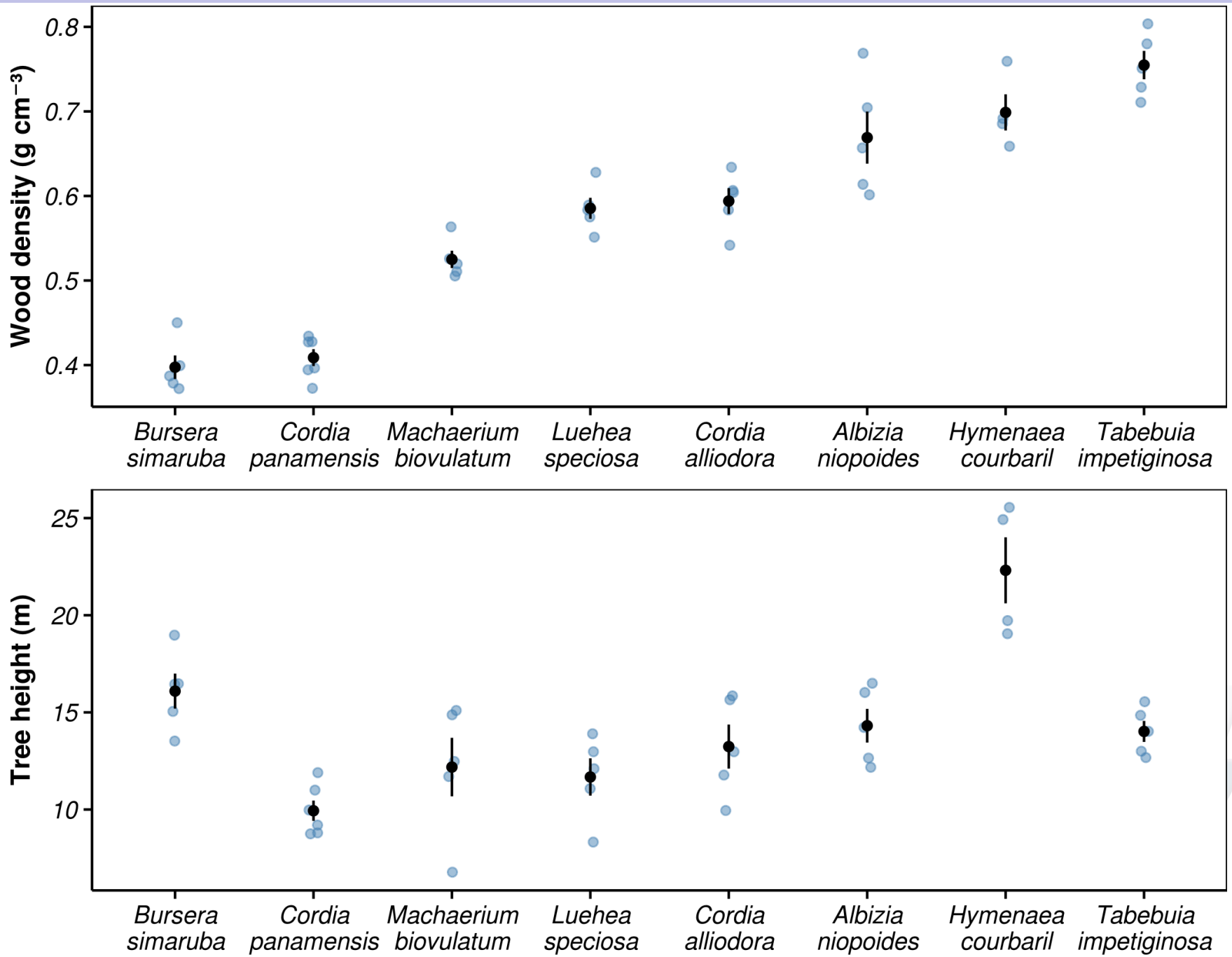
Wood density (g cm⁻³)
0.8
0.7
0.6
0.5
0.4
Bursera simaruba
Cordia panamensis
Machaerium biovulatum
Luehea speciosa
Cordia alliodora
Albizia niopoides
Hymenaea courbaril
Tabebuia impetiginosa
Tree height (m)
25
20
15
10
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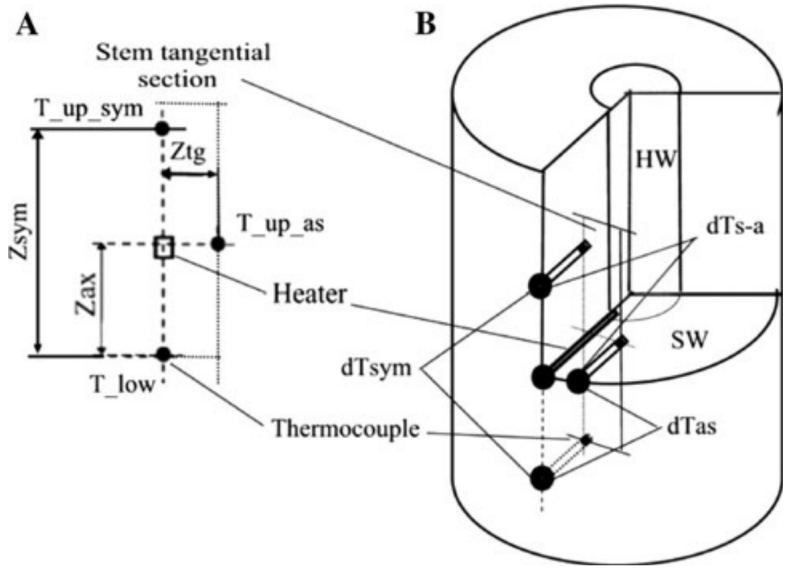
Heat field deformation sensors

Working principle:

- 1 heater and 3 temperature sensors inserted into wood
- Heater heats constantly with known caloric input
- Sap movement → faster heat transport in flow direction
- Temperature differences between sensors are used for estimation of sap flux density at different depths



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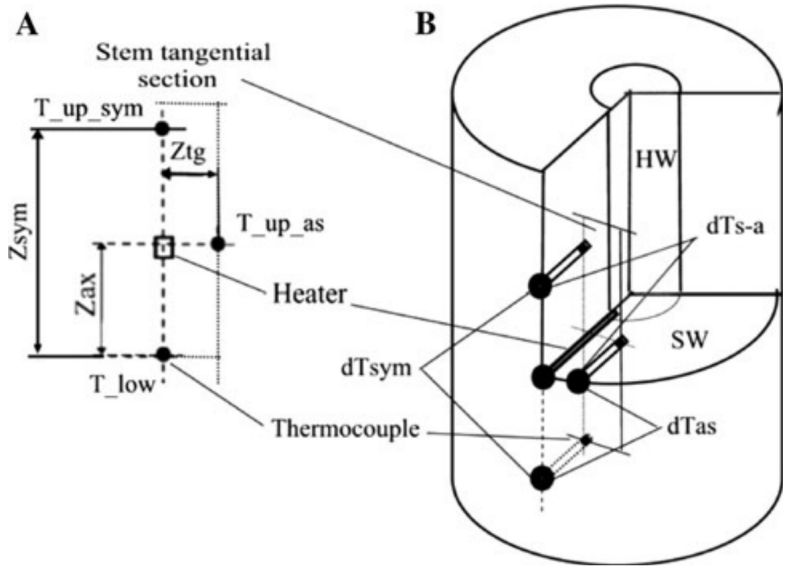

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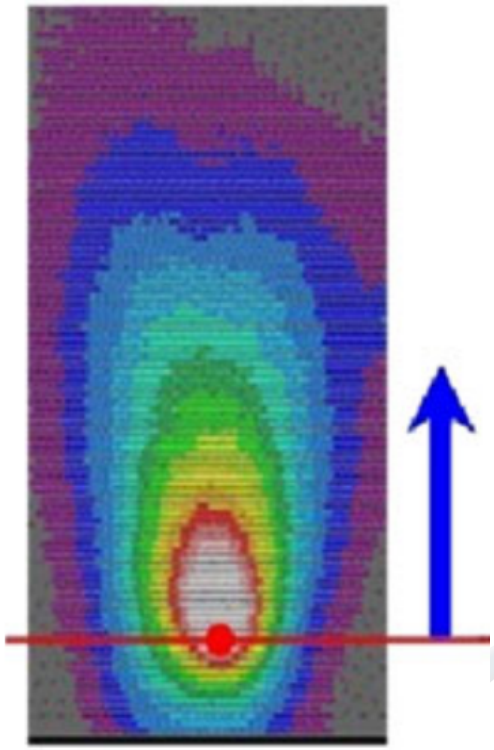

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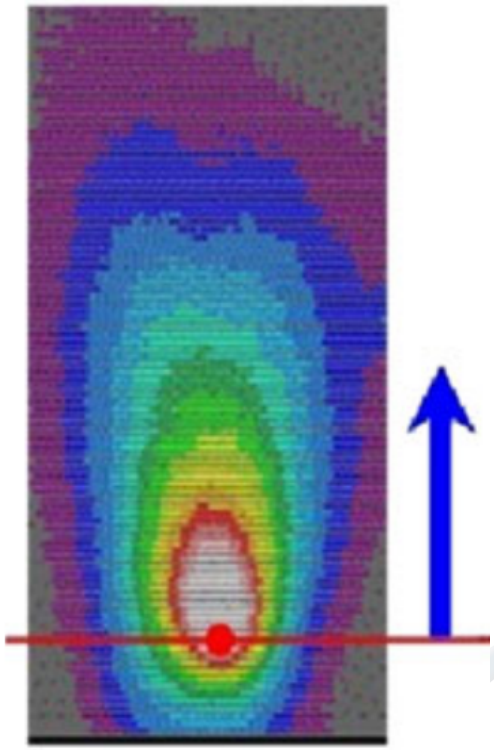

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Heat field deformation sensors

- Original idea: Comparison of sap flow and plant water use between species with different trait combinations

Heat field deformation sensors

- Problem: newer research indicates that
  a) The mechanistic explanation of the HFD method (Nadezhdina et al., 2012) is flawed (Vandegehuchte & Steppe, 2012)
  → species-specific calibration likely necessary in most cases
  b) HFD calibration parameters are not consistent within species (Fuchs et al., 2017)

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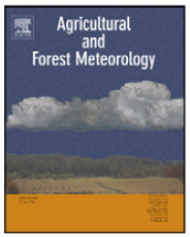

Short communication

Interpreting the Heat Field Deformation method: Erroneous use of thermal diffusivity and improved correlation between temperature ratio and sap flux density

Maurits W. Vandegehuchte*, Kathy Steppe

Laboratory of Plant Ecology, Faculty of Bioscience Engineering, Ghent University, Coupure links 653, 9000 Gent, Belgium

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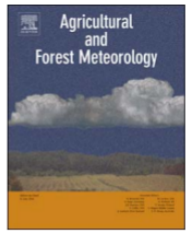

Calibration and comparison of thermal dissipation, heat ratio and heat field deformation sap flow probes for diffuse-porous trees

Sebastian Fuchs, Christoph Leuschner, Roman Link, Heinz Coners, Bernhard Schuldt*

Plant Ecology, Albrecht von Haller Institute for Plant Sciences, University of Goettingen, Untere Karspüle 2, 37073 Goettingen, Germany

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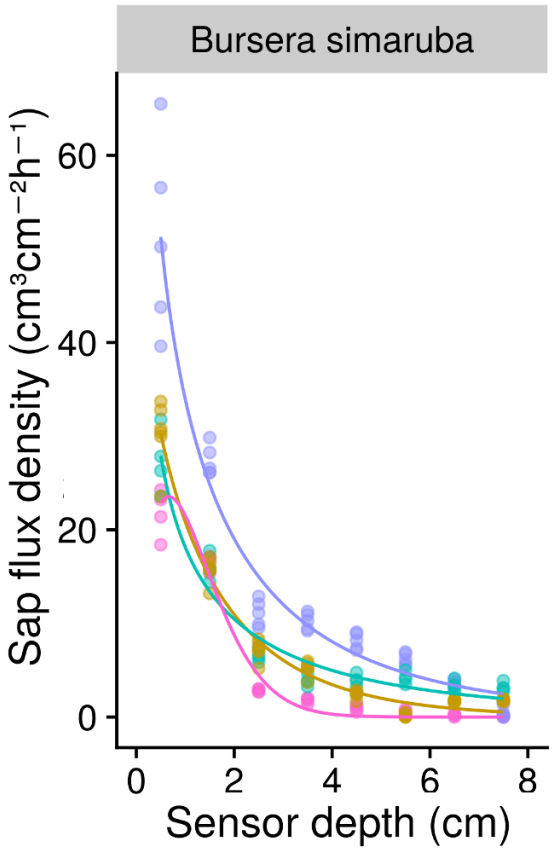
$\Rightarrow$ **Decision for analysis: better to put focus on radial gradients of sap flux**

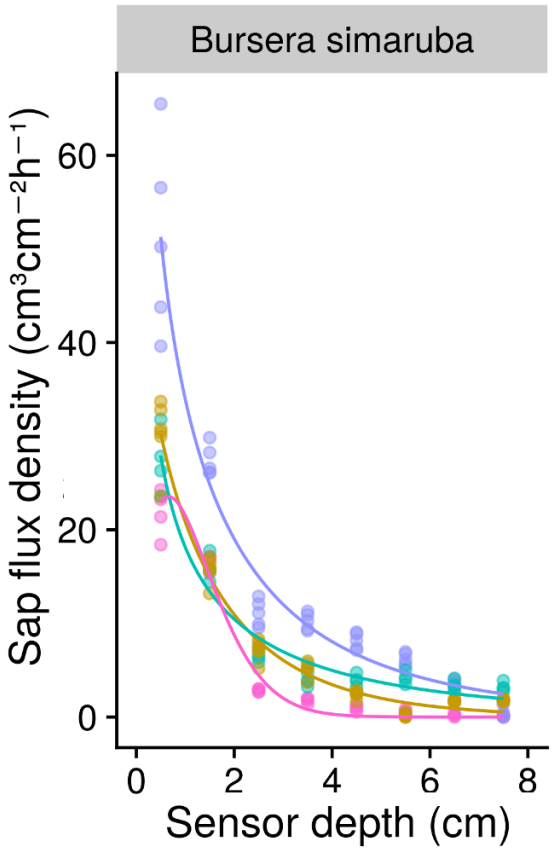
Research questions & hypotheses



- Radial sap flow gradients
  - very important for studies of plant water use
  - few methods take them into account
  - sensors are expensive and error-prone
  - species specific measurement: problematic in the tropics

⇒ **Question:** Is it possible to predict the shape of radial sap flow profiles based on tree traits?

Research questions & hypotheses



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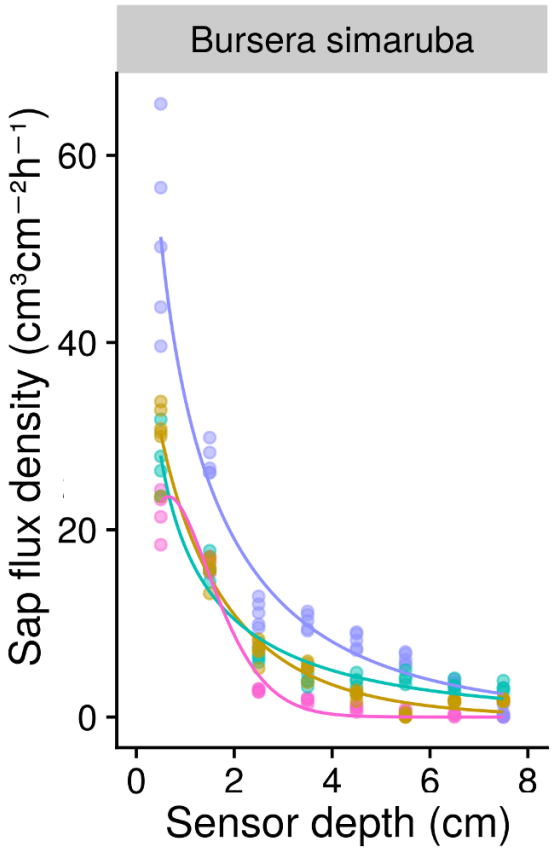

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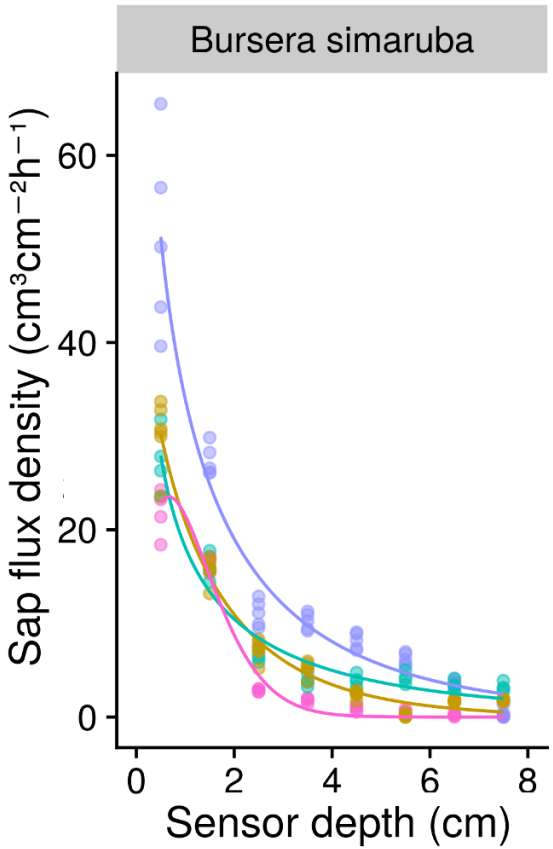

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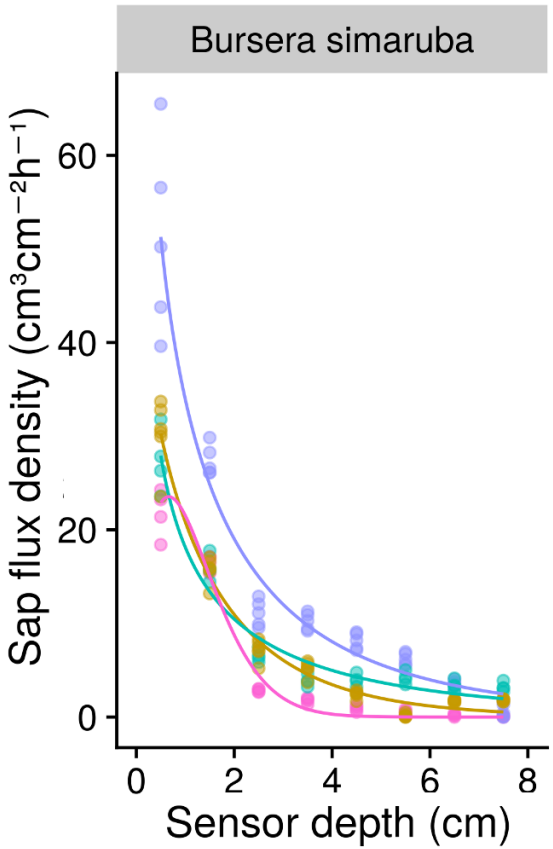

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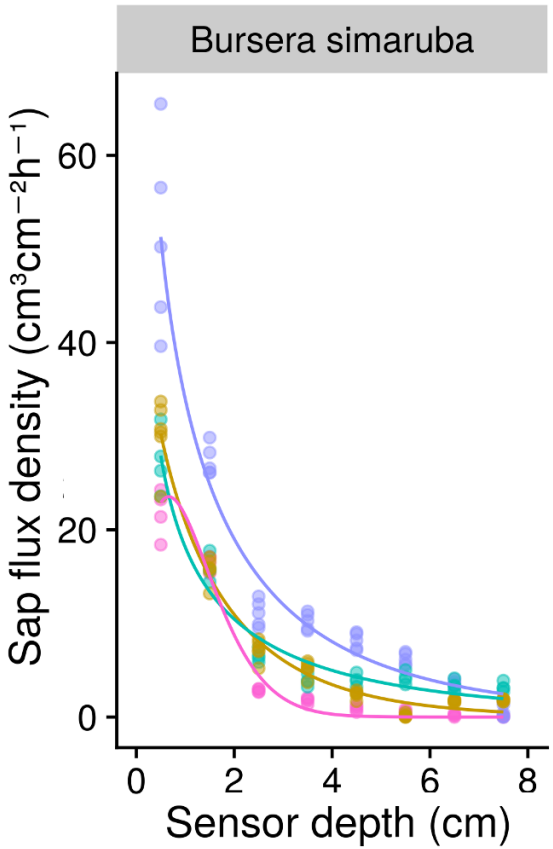

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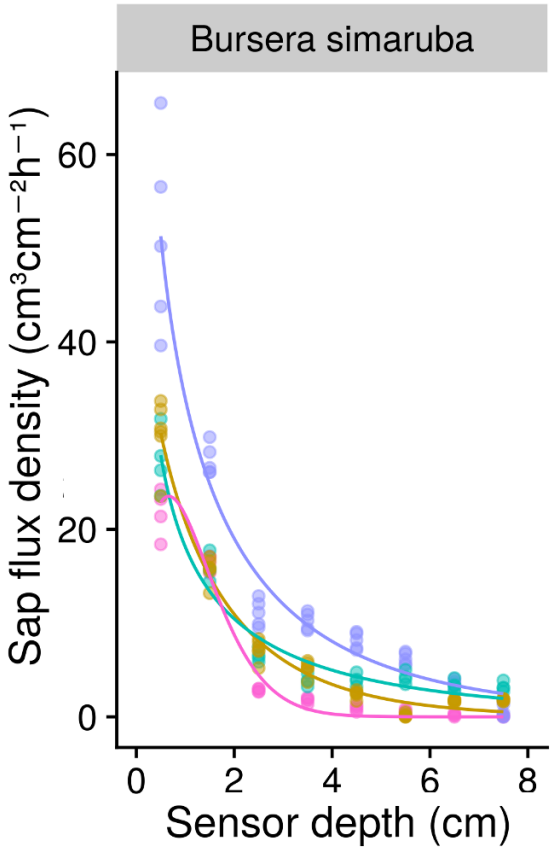
⇒ **Hypothesis:** The shape of radial sap flow profiles depends on **wood density** and **tree height**

Data analysis



- Nonlinear relationship
- Parameters that control the shape of the nonlinear relationship depend on other variables
- Hierarchical data structure (repeated observations in replicate trees from different species)

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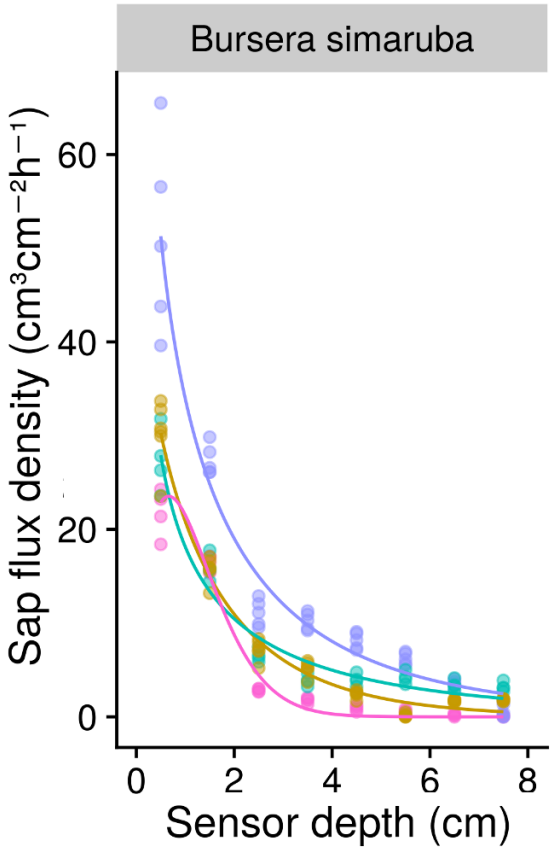

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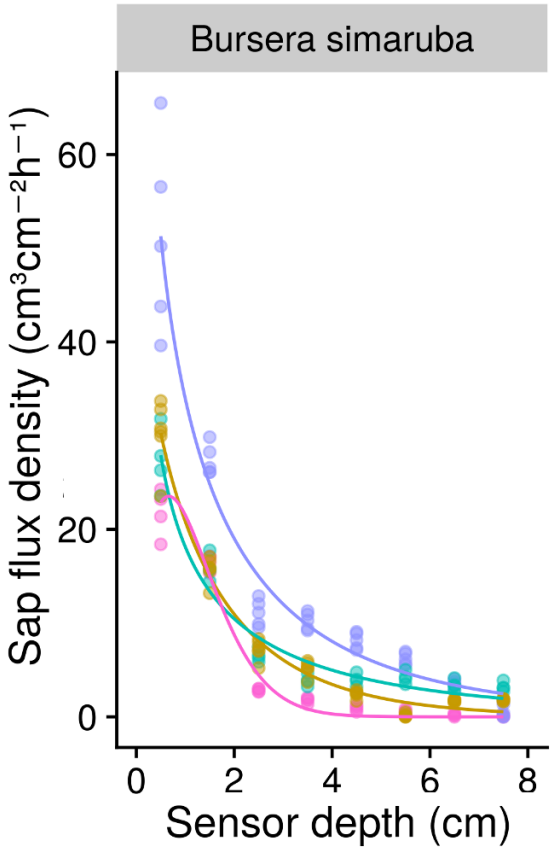

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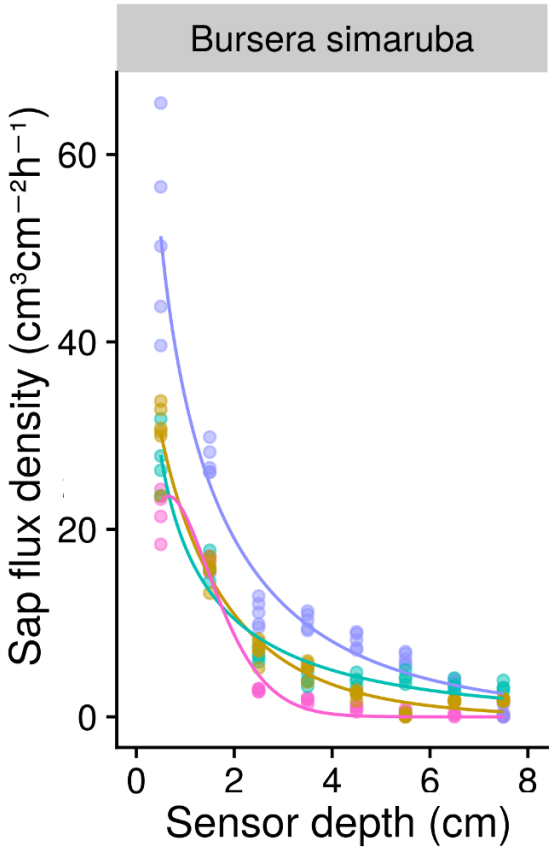

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$\Rightarrow$ **How to analyze?**

Data analysis

- Analysis based on **Bayesian nonlinear hierarchical models**
  - **First stage of the model:** Nonlinear relationship between sensor depth and predicted flux density modeled by density function of the Weibull distribution
  - **Second stage of the model:** Parameters of the Weibull distribution modeled as a function of wood density, tree height and their interaction, accounting for species and stem specific random variation

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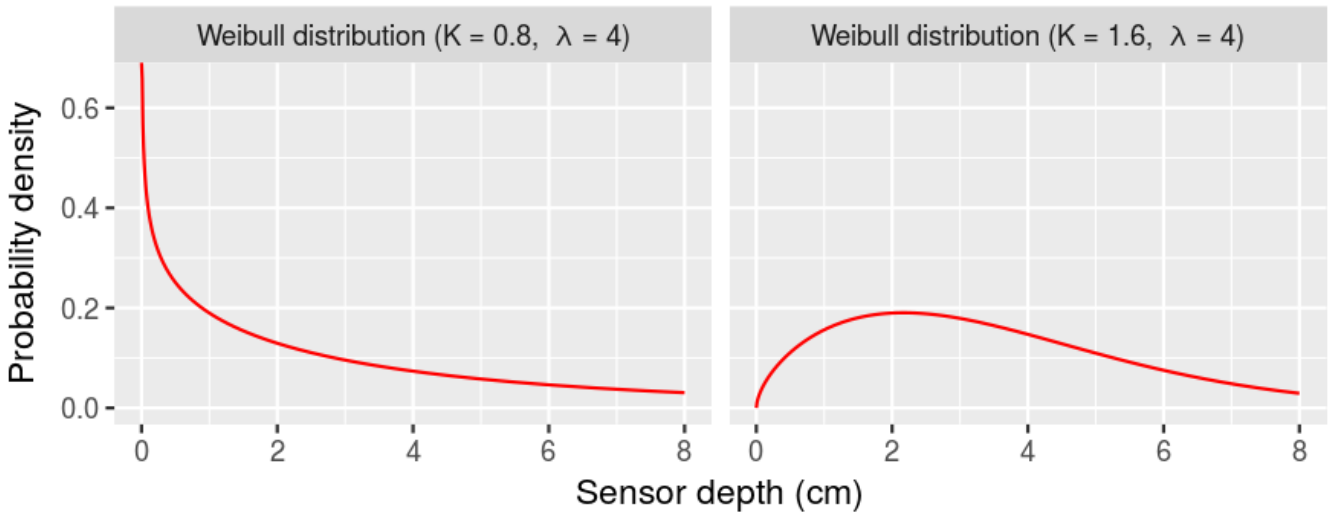

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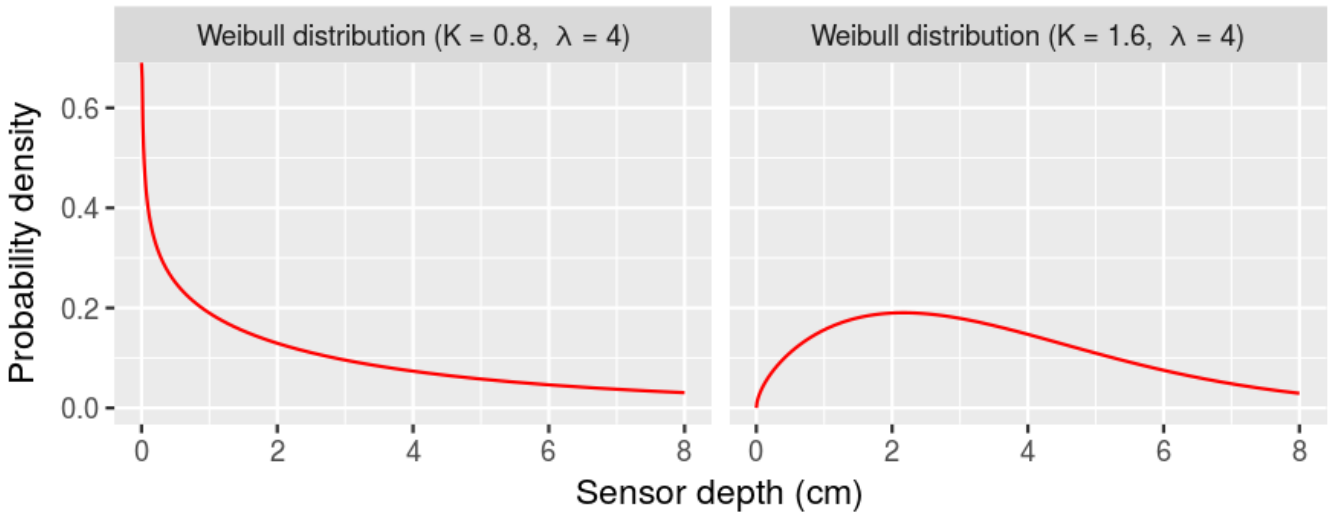

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  - Model fitting with the **Stan modeling language**
- Models still need tuning $\rightarrow$ shown results are from preliminary model based on R package `nlme`

Model equations of the preliminary model

Model equation

- $SFD_{ijk} \sim \text{Normal}(\mu_{ijk}, \sigma_{ijk})$
- $$\mu_{ijk} = c_{jk} \cdot \text{Weibull}(depth_{ijk} | \lambda_{jk}, K_{jk}) = c_{jk} \cdot \frac{K_{jk}}{\lambda_{jk}} \cdot \left(\frac{depth_{ijk}}{\lambda_{jk}}\right)^{K_{jk}-1} \cdot \exp\left(-\left(\frac{depth_{ijk}}{\lambda_{jk}}\right)^{K_{jk}}\right)$$

Parameter models

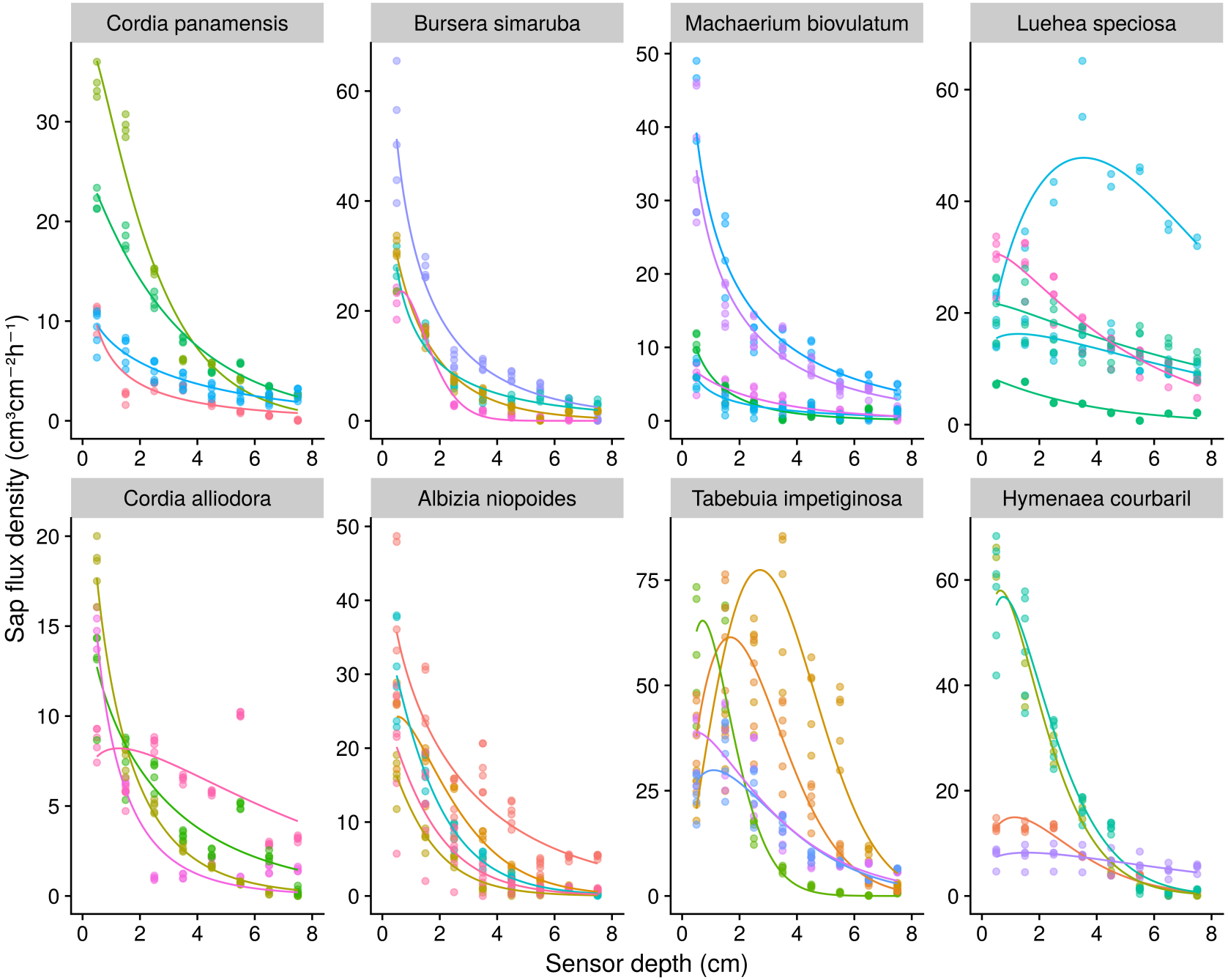
- $\lambda_{jk} = \exp(\beta_{\lambda 0} + \beta_{\lambda 1} \cdot WD + \beta_{\lambda 2} \cdot H + \beta_{\lambda 3} \cdot WD \cdot H + \epsilon_{j_\lambda} + \epsilon_{k_\lambda})$
- $K_{jk} = \exp(\beta_{K0} + \beta_{K1} \cdot WD + \beta_{K2} \cdot H + \beta_{K3} \cdot WD \cdot H + \epsilon_{j_K} + \epsilon_{k_K})$
- $c_{jk} = \exp(c_0 + \epsilon_{j_c})$

Random effects

- $\epsilon_j \sim \text{MultiNormal}(0, \Sigma_j)$
- $\epsilon_k \sim \text{MultiNormal}(0, \Sigma_k)$

Variance covariates

- $\sigma^2_{ijk} = \sigma^2_0 \cdot \exp(2 \cdot \delta \cdot \mu_{ijk})$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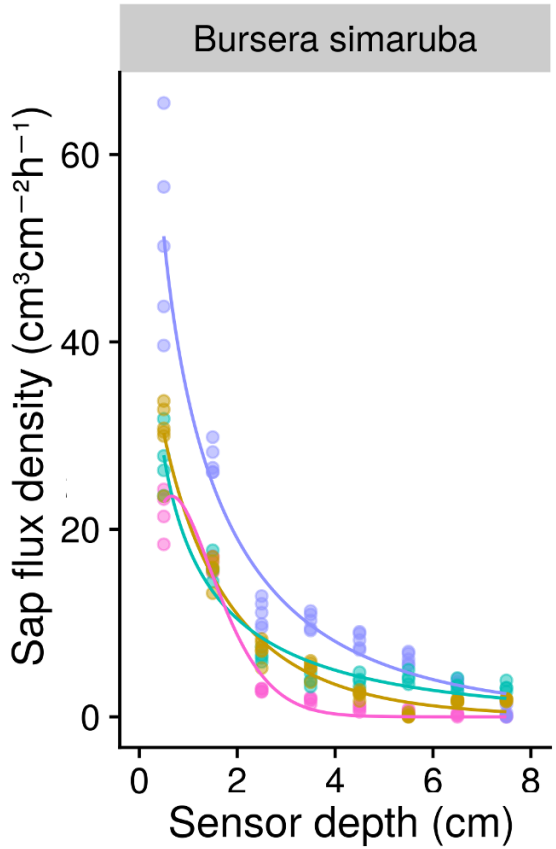
Hymenaea courbaril
Sap flux density (cm³cm⁻²h⁻¹)
Sensor depth (cm)

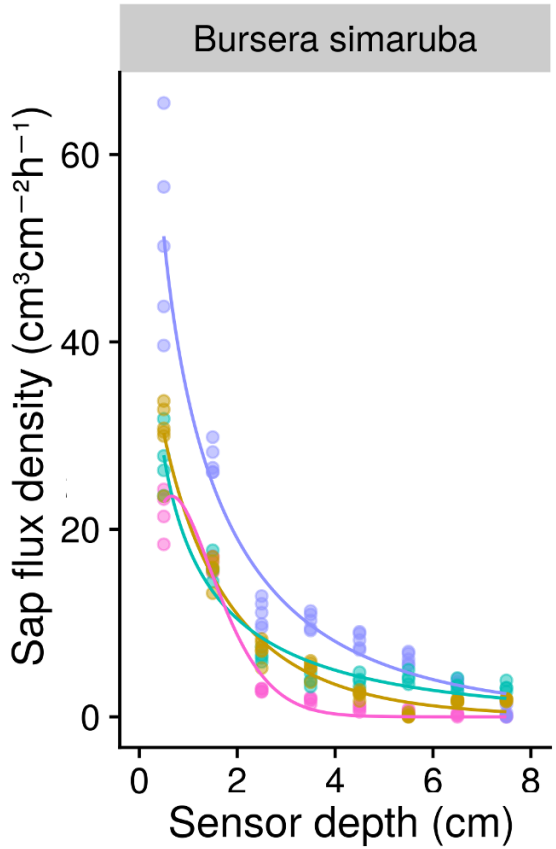
Preliminary results I - predicted profiles

- Model explains a large part of the observed variance in the dataset (conditional pseudo-$R^2 = 0.918$)
- Most of this variance is explained by random differences between species and stems (marginal pseudo-$R^2 = 0.329$)

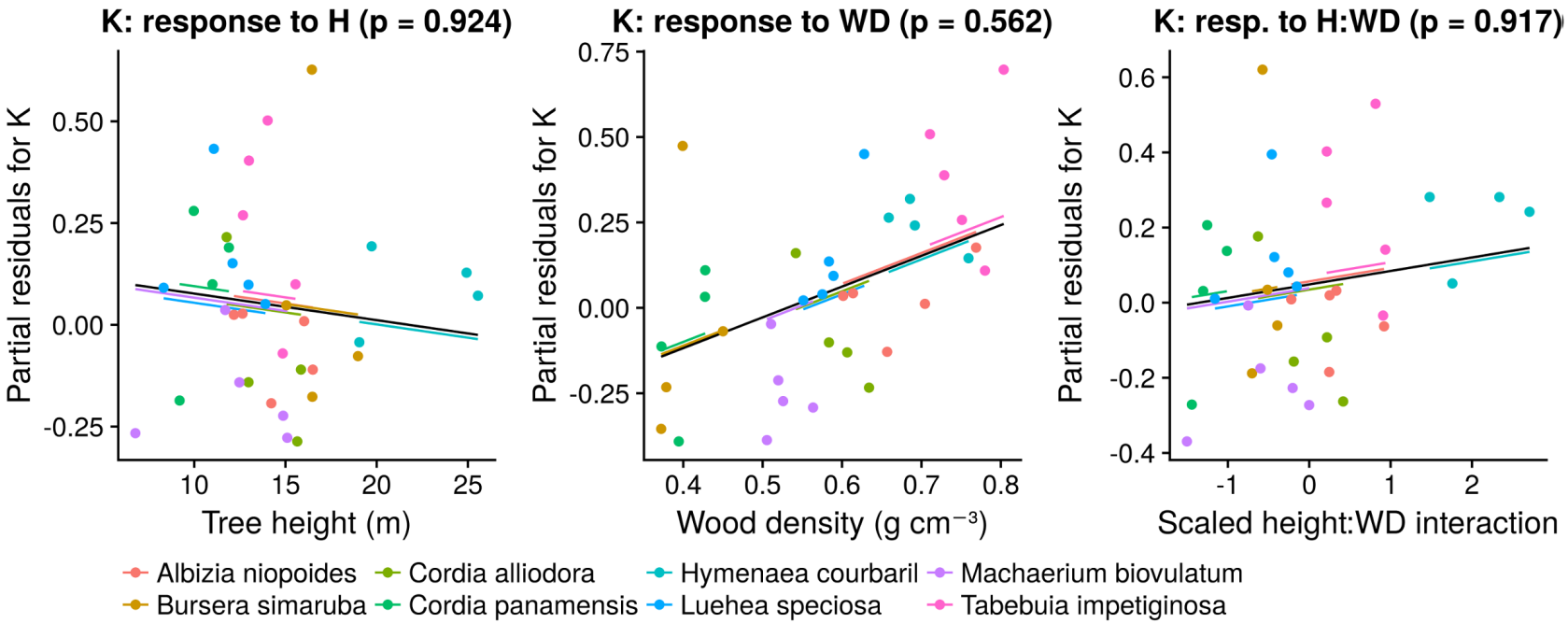


Preliminary results I - predicted profiles

- Model explains a large part of the observed variance in the dataset (conditional pseudo-$R^2 = 0.918$)
- Most of this variance is explained by random differences between species and stems (marginal pseudo-$R^2 = 0.329$)



Preliminary results II - parameter models



- **Weibull shape parameter K**
  - No significant height- and wood density effects

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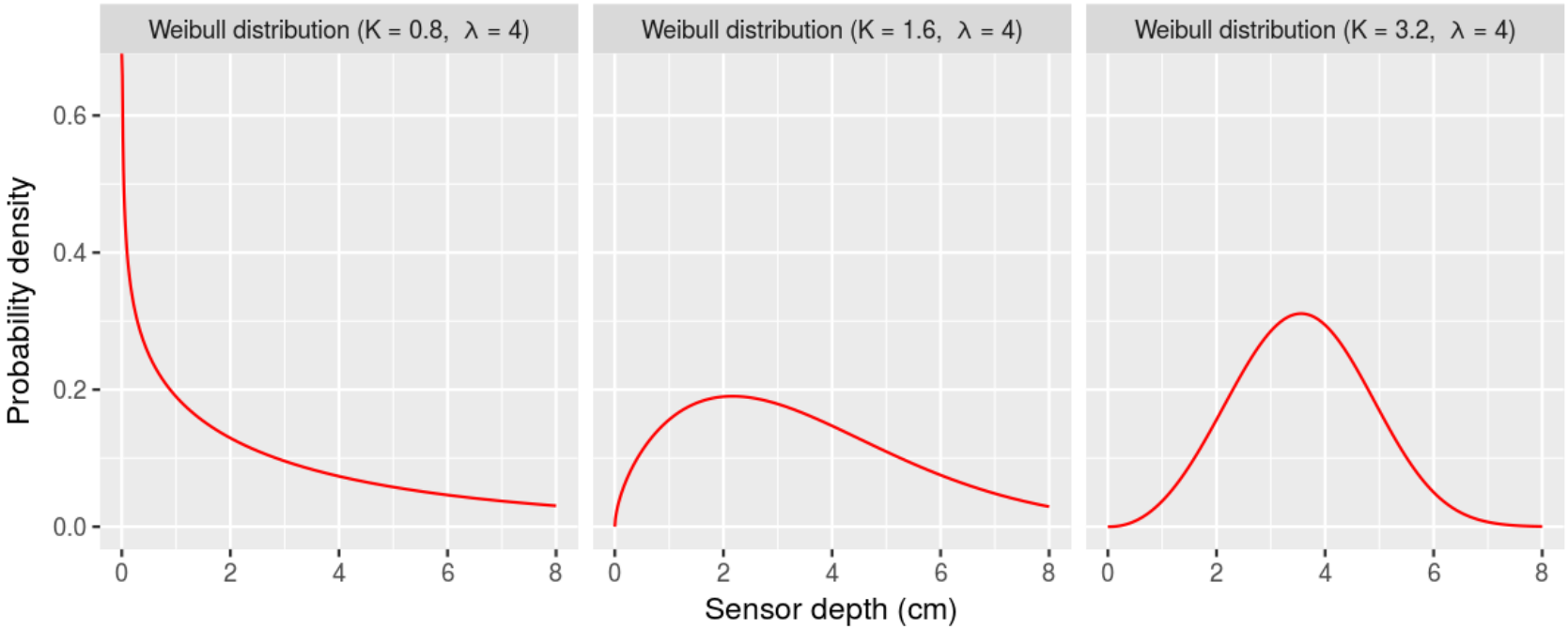

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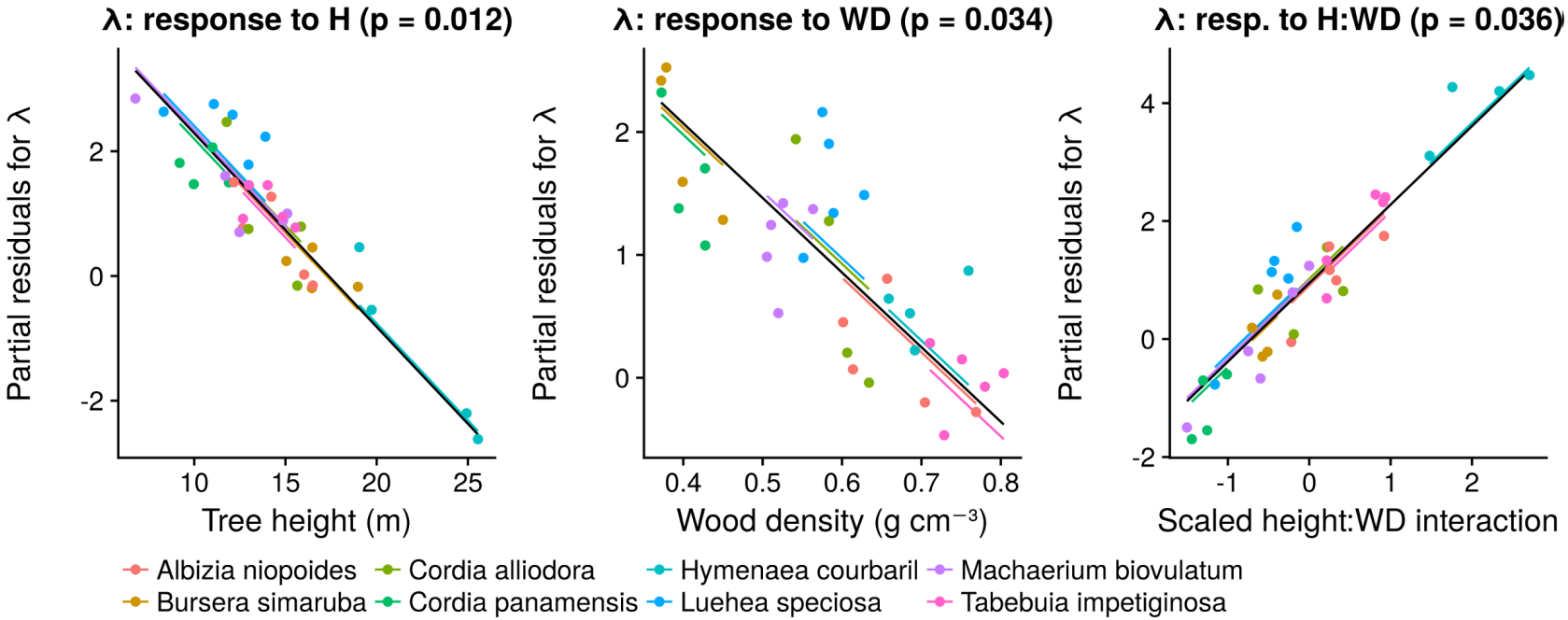

- **Weibull scale parameter λ**
  - Decreases significantly with tree height and wood density, but significantly less so in trees that are both large AND have hard wood

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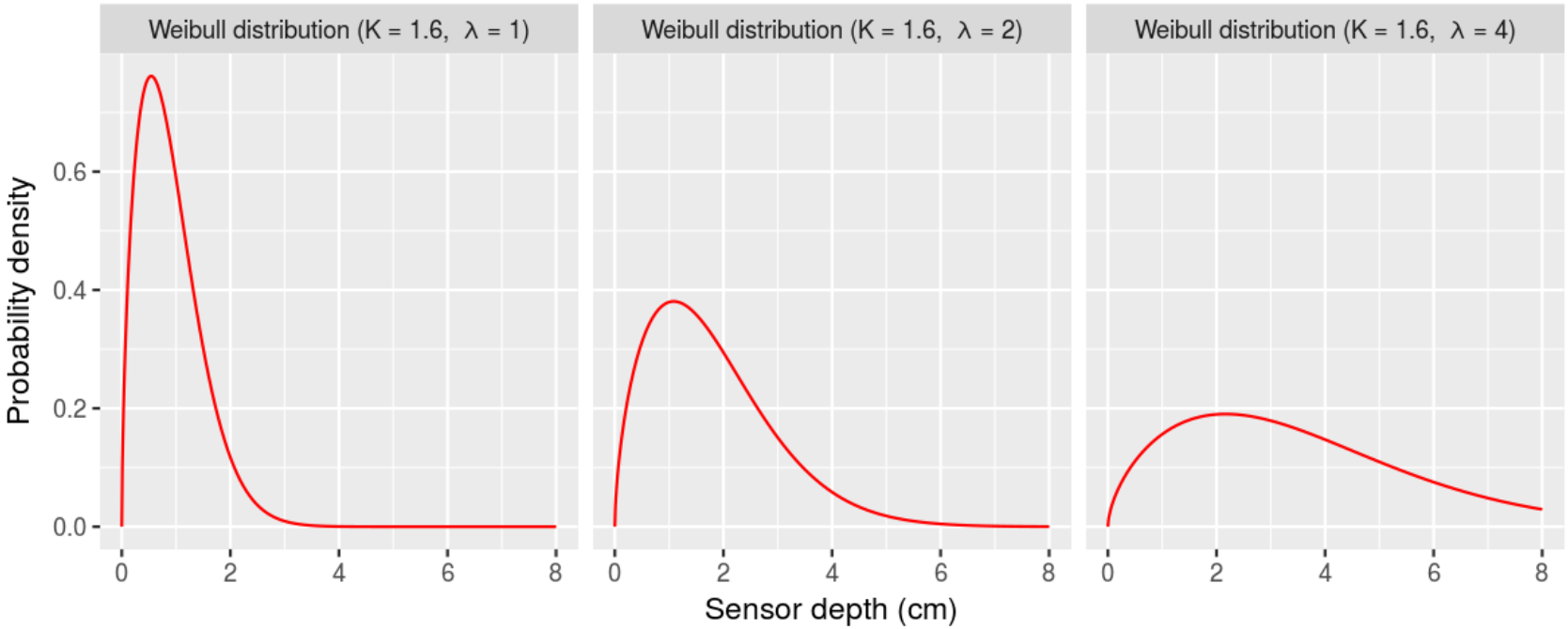

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Radial sap flow profiles - Conclusions

- Shape of the profile significantly depends on height and wood density
- Model describes observed radial profiles very well
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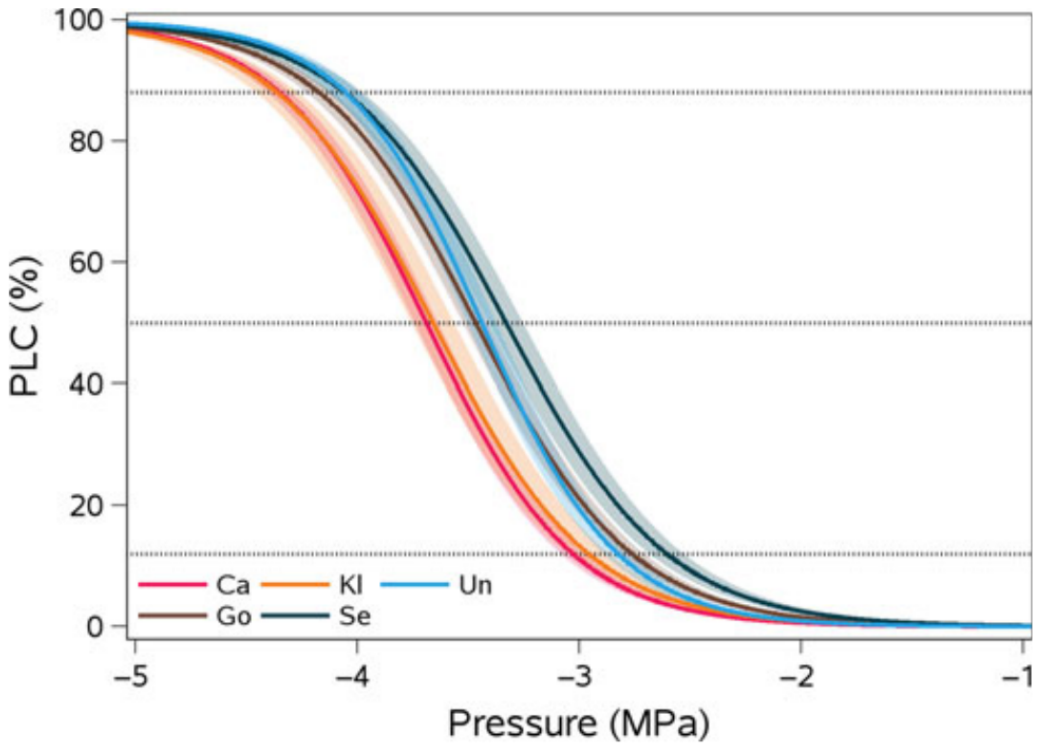
Second chapter: vulnerability curves

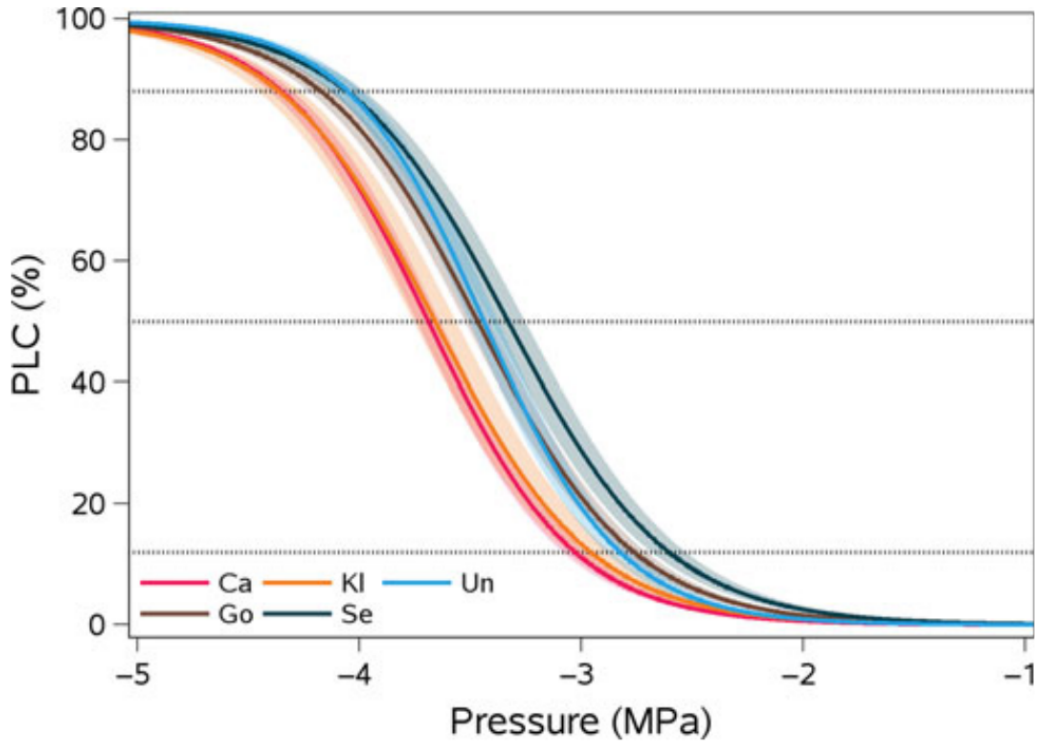


- Relationship between water potential and percentage loss of conductivity (PLC)

→ shows the loss of conductive function under increasingly dry conditions

Image source: Schuldt et al., 2015

Second chapter: vulnerability curves



- Parameters of vulnerability curves: important predictors of drought response
  - **P_{50}:** At what pressure does a plant lose 50% of its conductivity?
  - **Slope:** How fast does this loss occur?

Image source: Schuldt et al., 2015

Second chapter: vulnerability curves

- Vulnerability curves of replicate samples from 30 trees of 10 tropical forest species from the Osa peninsula (56 in total)
- Collection of upper canopy branches in two campaigns in the rainy seasons of 2016 and 2017
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Foto: http://sylvain-delzon.com/caviplace/

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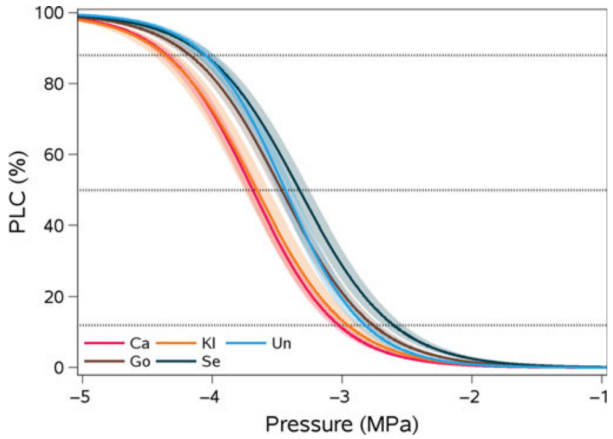
Research questions & hypotheses

- Plant vulnerability to embolism can be predicted by structural, functional and wood anatomical traits

Data analysis



- Nonlinear relationship
- Parameters that control the shape of the nonlinear relationship (P50 and slope) depend on other variables
- Hierarchical data structure (repeated observations on replicate samples from replicate trees belonging to different species)

Image source: Schuldt et al., 2015

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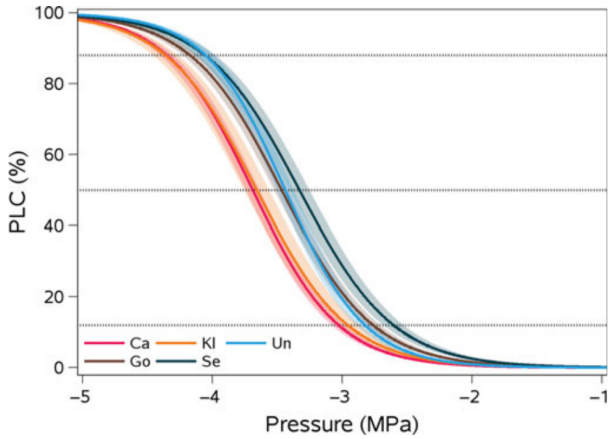

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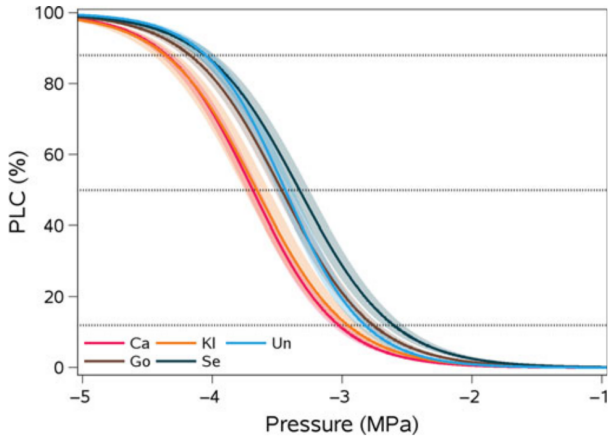

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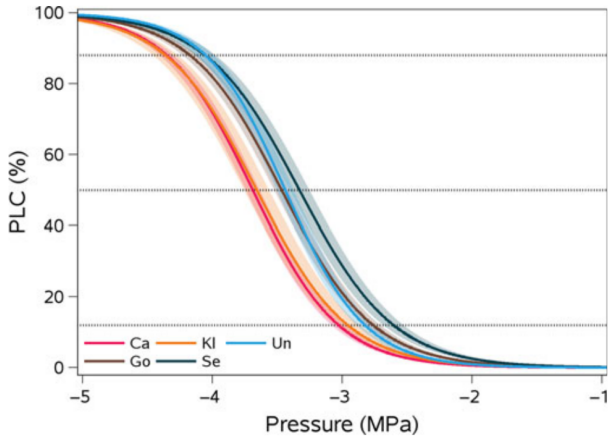

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⇒ **Nonlinear hierarchical models**
(analogous to models for radial sap flow profiles)

Image source: Schuldt et al., 2015

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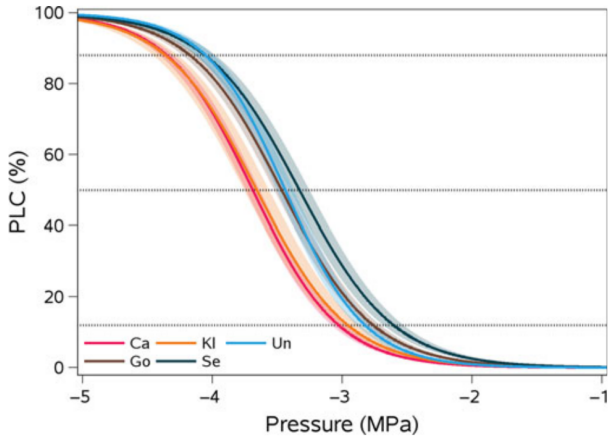

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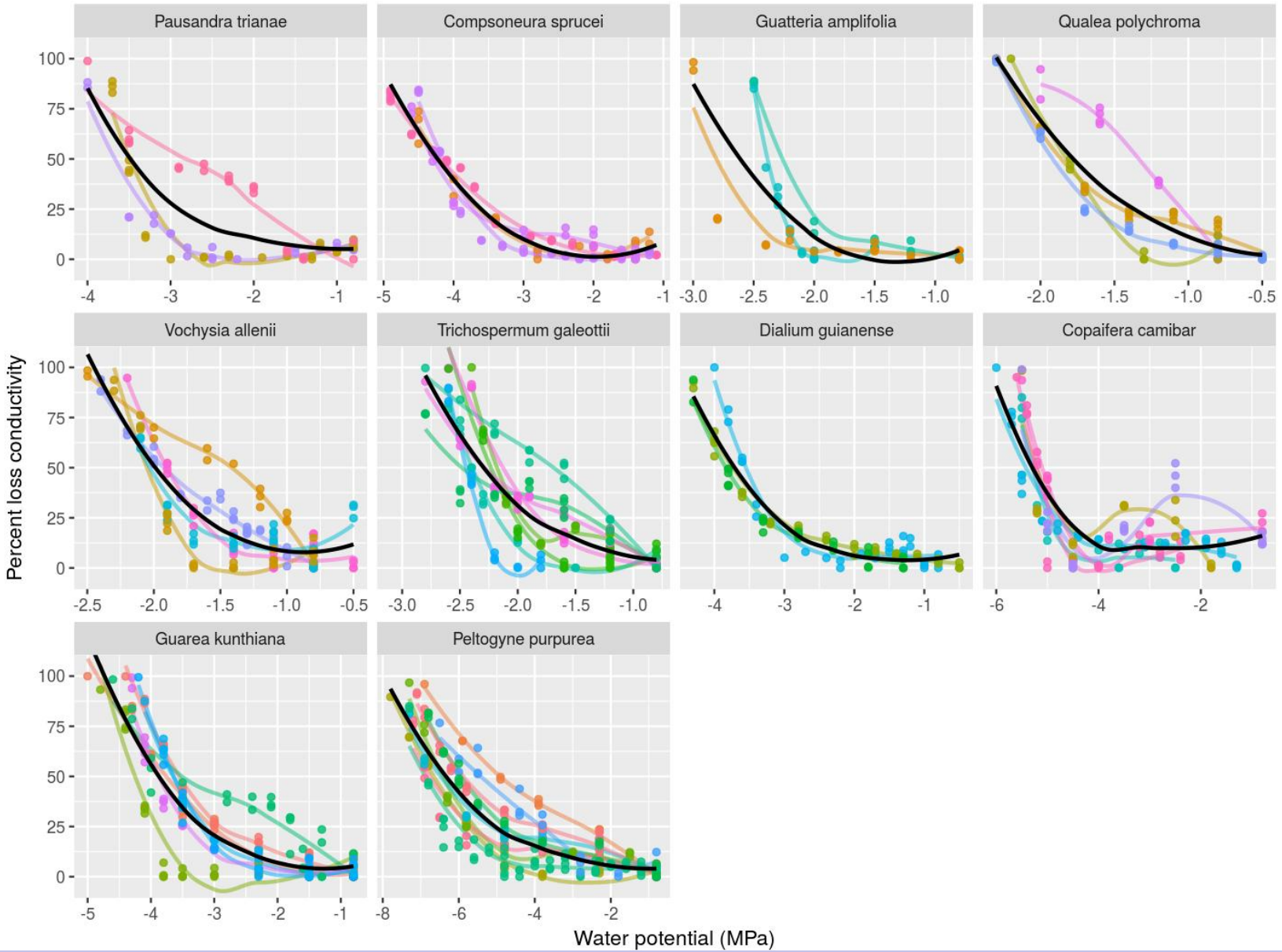
⇒ **Data analysis in progress**

Image source: Schuldt et al., 2015

Observed vulnerability curves



The big picture

- Do structural, functional and wood anatomical traits explain changes in productivity and hydraulic traits?
- How are these changes related to the rainfall gradient?

Growth data

- short description
- picture

Wood anatomy

- short description
- picture

Non-structural carbohydrates

- short description
- picture
- data not available so far

Research questions & hypotheses

- Lots and lots of hypotheses

Data analysis

- Short explanation of structural equation models

Meta-model & causal diagram

- figures on one or two slides

Example for SEM: Martyna's paper

- Meta-model, causal diagram & final path model

Summary

- Sap flow
- Vulnerability curves
- SEM

Thanks & goodbye

- Names of assistants (pictures?)

References

- **Fuchs S, Leuschner C, Link R, Coners H, Schuldt B, 2017.** Calibration and comparison of thermal dissipation, heat ratio and heat field deformation sap flow probes for diffuse-porous trees, *Agricultural and Forest Meteorology* **244–245**,151-161. https://doi.org/10.1016/j.agrformet.2017.04.003..