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

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Structure of the PhD project

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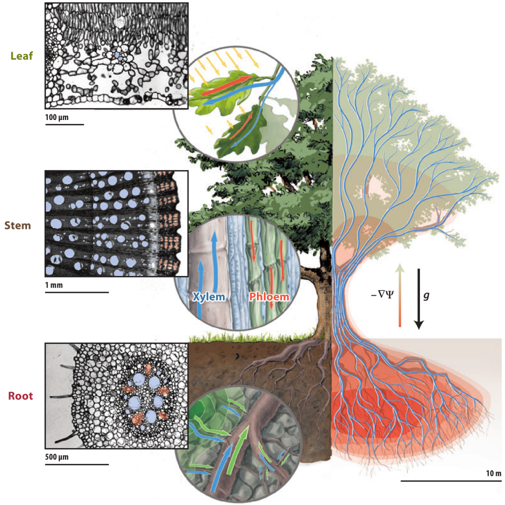
- **Bonus Chapter:** Maximum-likelihood estimation of xylem vessel lengths: **Not in the focus of this presentation!**

Water transport in plants



- Driving force: gradient in water potentials
- Continuous water columns held together by *cohesion-tension-mechanism*

Image source: Stroock et al., 2014

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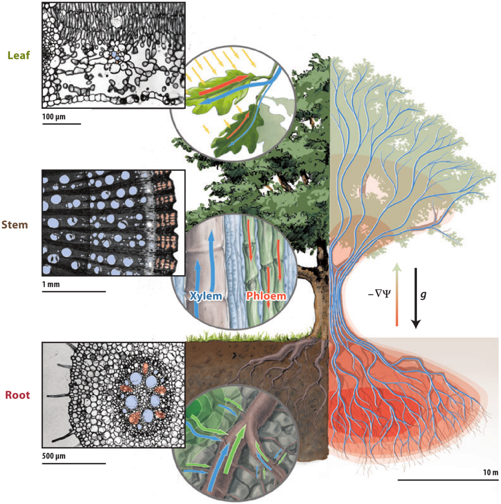

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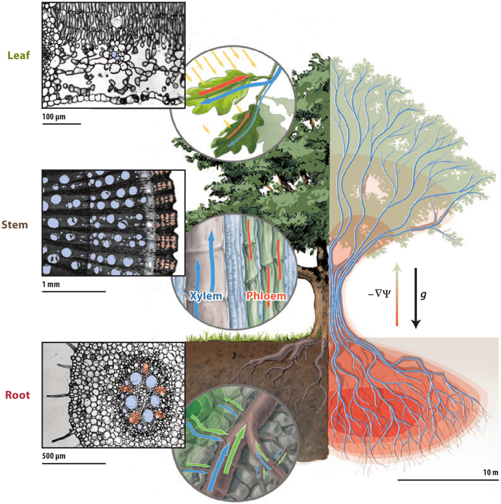

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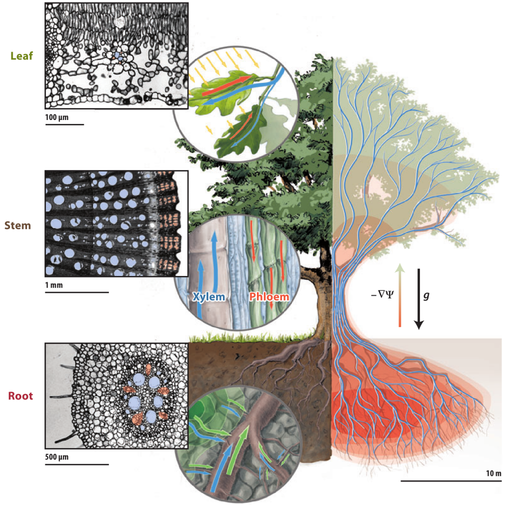

- Driving force: gradient in water potentials
- Continuous water columns held together by *cohesion-tension-mechanism*

→ Liquid under tension: **metastable state**

→ If negative pressure too high: **risk of embolism & loss of conductance**

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Plant water relations in the tropics

- **Global change in the tropics**
  - Rise in temperatures
  - Regionally decreasing precipitation

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- **Focus of research:**
  - How do tropical trees respond to drought on an ecophysiological level?

  ⇒ More mechanistical understanding of drought responses necessary (e.g. to improve global climate projections)

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 (only mature trees)

⇒ 40 trees per site, 200 trees in total

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  - 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
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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)
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→ Plot-based comparisons are difficult

⇒ Not that important for my (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
- Measured with the Heat Field Deformation (HFD) method

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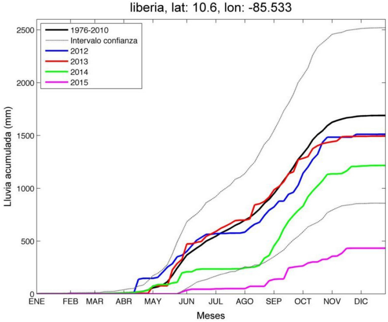

Image source: Instituto Meteorológico Nacional de Costa Rica

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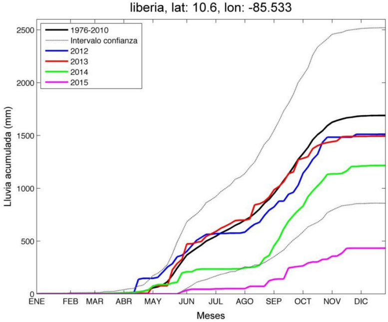

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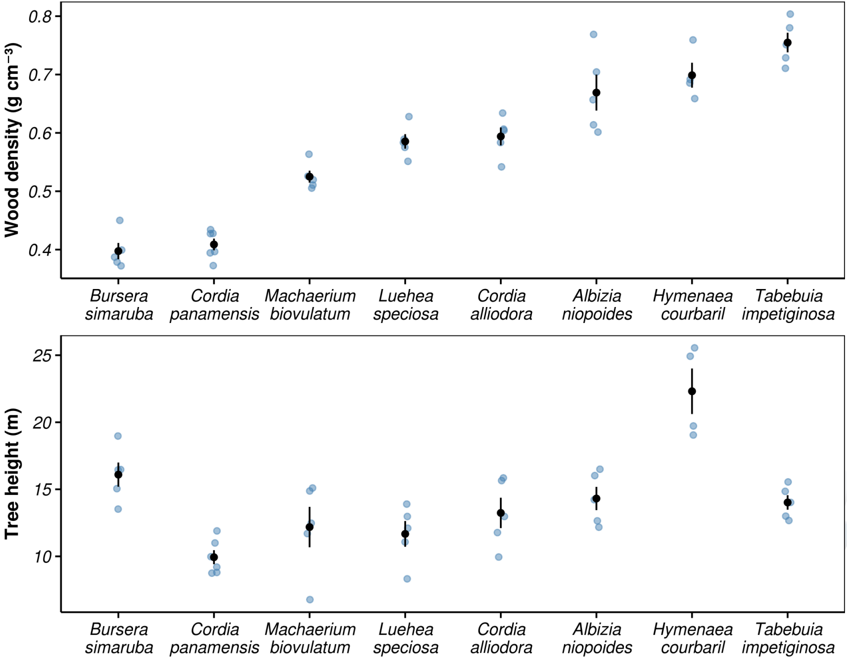
Wood density (g cm^{-3})
0.8
0.7
0.6
0.5
0.4
Bursera simaruba
Cordia panamensis
Machaerium biovulatum
Luehea speciosa
Cordia alliodora
Albizia niopoides
Hymenaea courbaril
Tabebuia impetiginosa
Tree height (m)
25
20
15
10
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First chapter: radial sap flow profiles

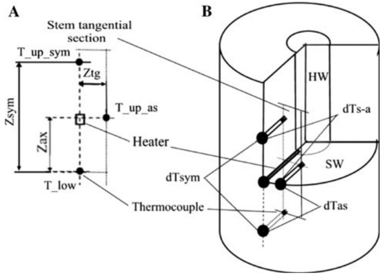
Additionally measured:

- Soil water content
  - 1 measurement for each of the 4 campaigns
  - 1 soil sample per subplot (4×45 in total)
- Vertical microclimate
  - Temperature + air humidity tracked each 10 min with *iButtons*
  - Measured from ground level to canopy in 5 m steps
  - 3 measurement lines

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 to estimate sap flux density at different depths



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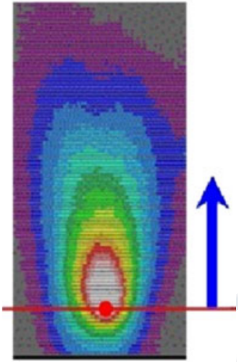

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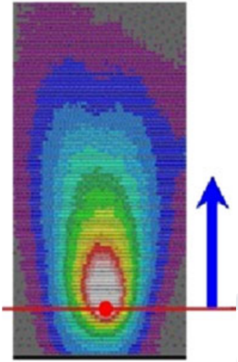

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Heat field deformation sensors

- 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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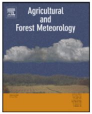

Short communication

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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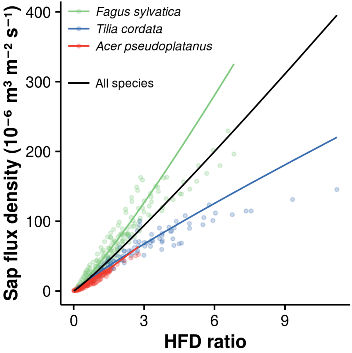

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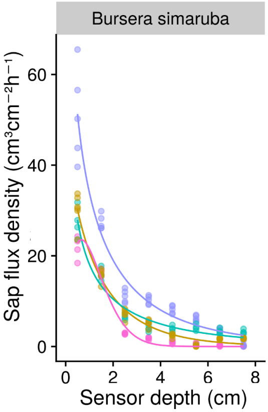
$\Rightarrow$ **Decision for analysis: better to put focus on radial gradients of sap flux**

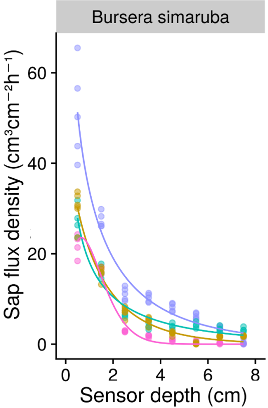
Research questions & hypotheses



- 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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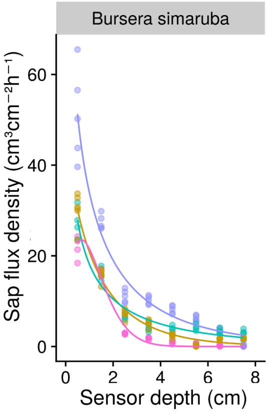

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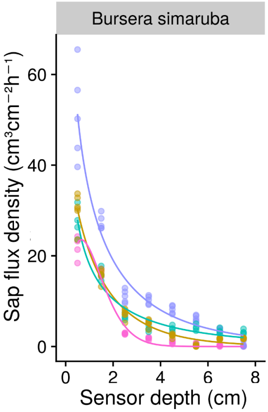

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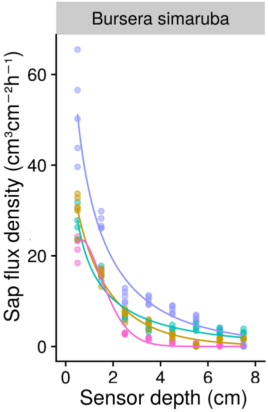

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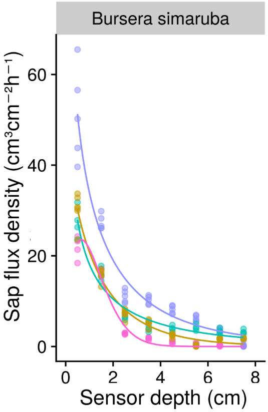

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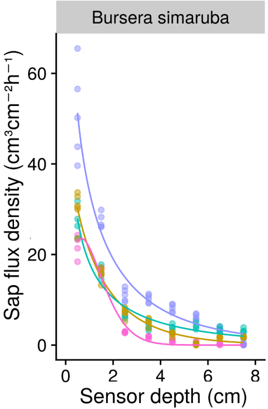
⇒ **Hypothesis:** The shape of radial sap flow profiles depends on **wood density** and **tree height**

Data analysis



How to analyze sap flow profiles?

- Observational unit: daily averages of sap flux density
- 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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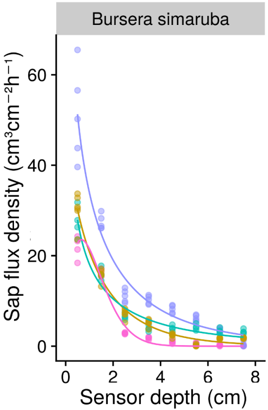

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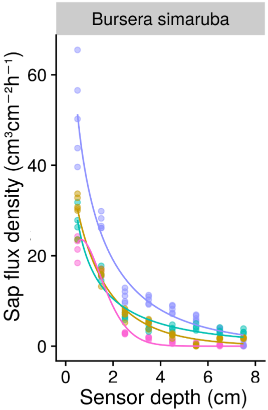

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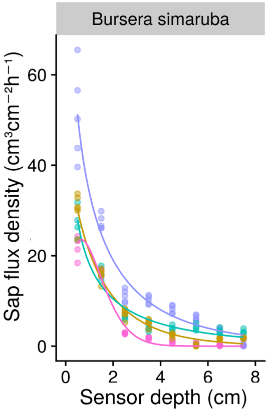

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- Analysis based on **Bayesian nonlinear hierarchical models**
  - **First stage of the model:** Nonlinear relationship between sensor depth and predicted flux density modeled with the density function of the Weibull distribution
  - **Second stage 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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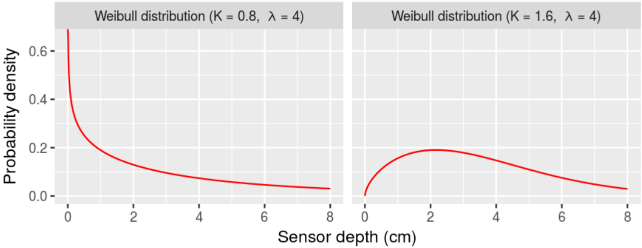

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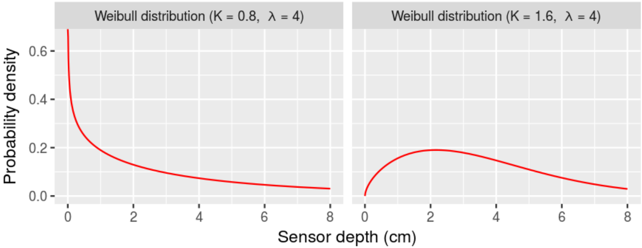

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  - Model fitting with the **Stan modeling language**
- Models still need tuning → shown results are from preliminary model based on R package `nlme`

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

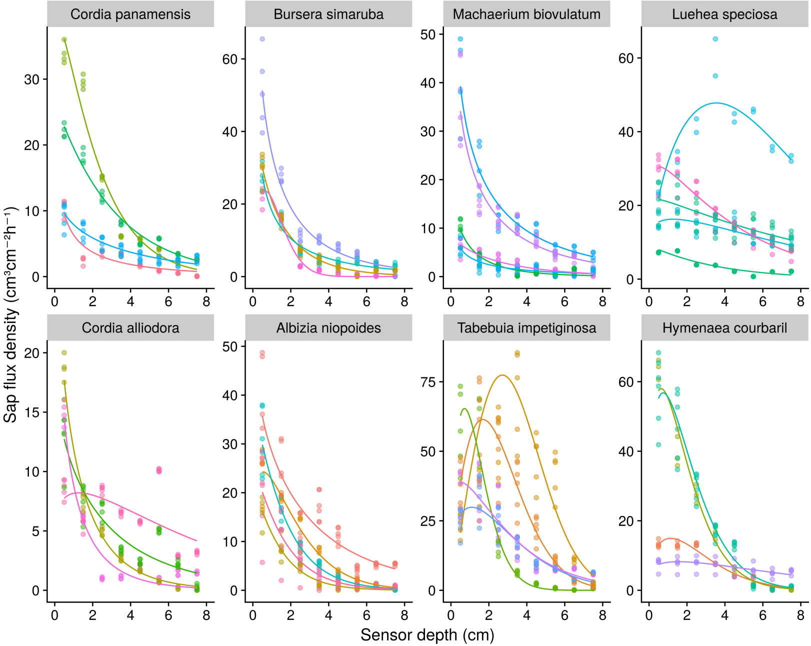
- $\lambda_{jk} = \exp(\beta_{\lambda 0} + \beta_{\lambda 1} \cdot WD + \beta_{\lambda 2} \cdot H + \beta_{\lambda 3} \cdot WD \cdot H + \epsilon_{j_\lambda} + \epsilon_{k_\lambda})$
- $K_{jk} = \exp(\beta_{K0} + \beta_{K1} \cdot WD + \beta_{K2} \cdot H + \beta_{K3} \cdot WD \cdot H + \epsilon_{j_K}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

Random effects

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

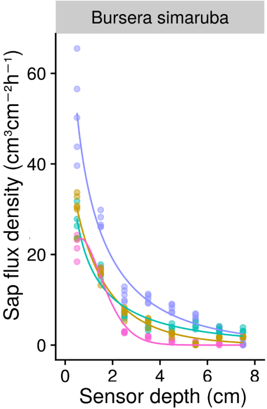
Variance covariates

- $\sigma_{ijk}^2 = \sigma_0^2 \cdot \exp(2 \cdot \delta \cdot \mu_{ijk})$


Cordia panamensis
Bursera simaruba
Machaerium biovulatum
Luehea speciosa
Cordia alliodora
Albizia niopoides
Tabebuia impetiginosa
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-$R^2 = 0.329$)



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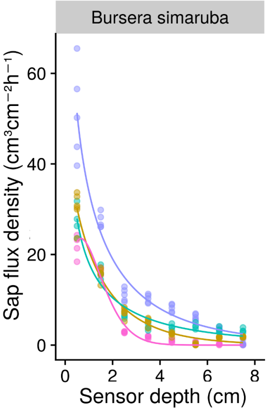
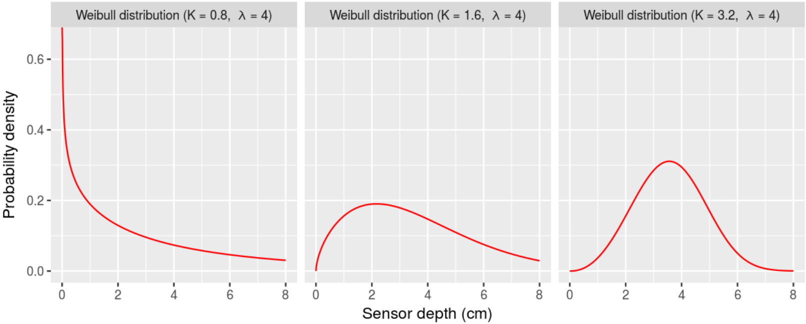
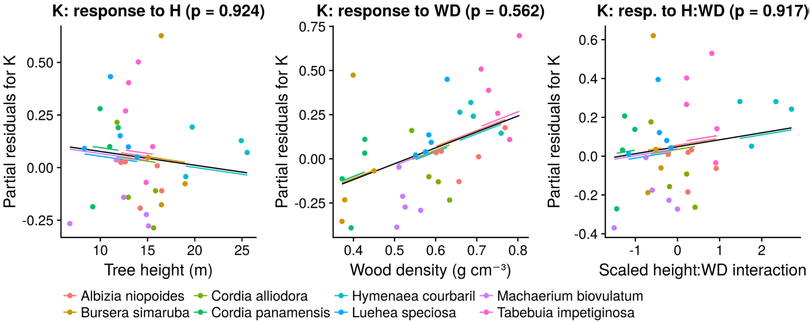


Preliminary results II - parameter model for K



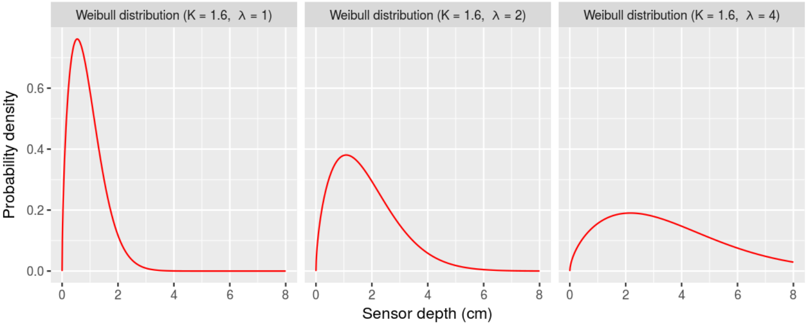
- **Weibull shape parameter K**

Preliminary results II - parameter model for K



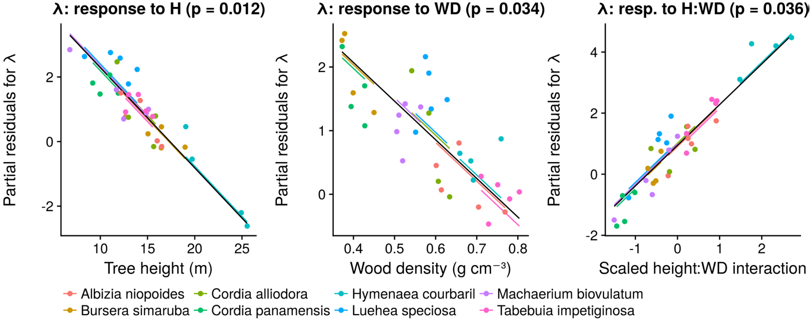
- **Weibull shape parameter K**
  - No significant height- and wood density effects

Preliminary results II - parameter model for λ



- **Weibull scale parameter λ**

Preliminary results II - parameter model for λ



- **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

Radial sap flow profiles - Conclusions

- Shape of the profile significantly depends on height and wood density
- Model describes observed radial profiles very well
- Explained variance is much lower when predicting onto new trees because of the high stem-specific variability
- Inclusion of other predictors might improve predictions (and consequently increase the value of the model for studies of plant water use)

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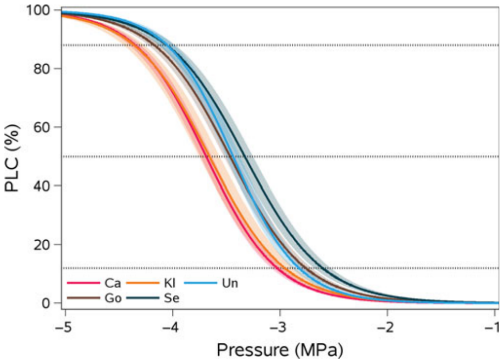
Second chapter: vulnerability curves

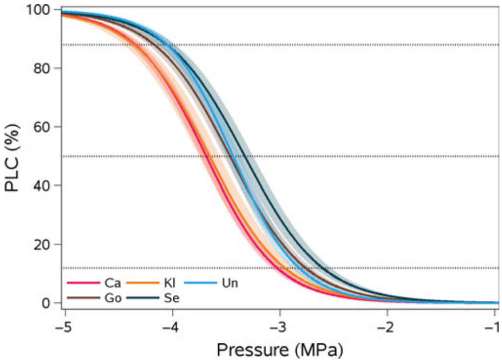


- Vulnerability curves: relationship between water potential and percentage loss of conductivity (PLC)

→ curve describes the loss of conductive function under increasingly dry conditions

Image source: Schuldt et al., 2016

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., 2016

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
- Measured with the Cavitron method using a novel 1 m rotor (courtesy of the lab of Sylvain Delzon, Bordeaux)

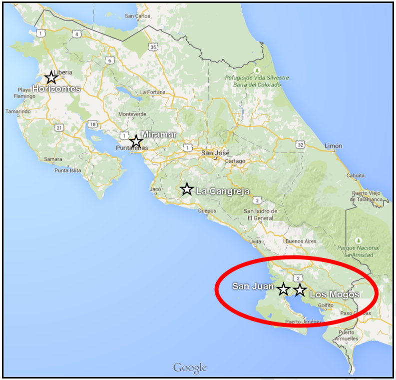


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Foto: `http://sylvain-delzon.com/caviplace/`

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Second chapter: vulnerability curves

Additionally measured for each tree:

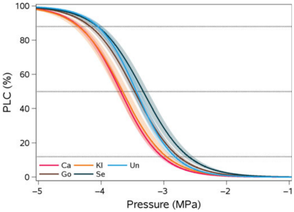
- Maximum vessel length (1 per tree)
- Leaf nutrient contents (1 per sample)
- Specific leaf area (1 per sample)
- Anatomy of branch wood (2 per sample)
- Huber value (1 per sample)
- Branch non-structural carbohydrate storage (1 per tree)

Hypothesis

The parameters of vulnerability curves are significantly related to plant structural, functional and wood anatomical traits:

- Tree size (height and diameter)
- Wood density
- Vessel diameter & vessel density

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., 2016

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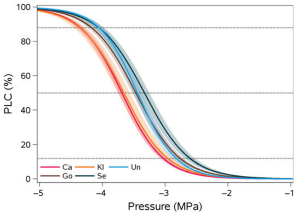

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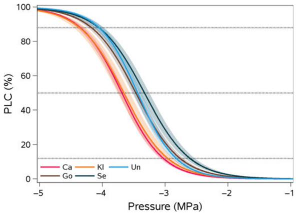

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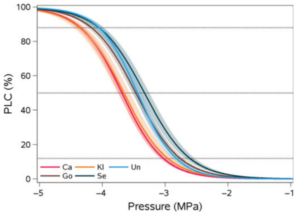

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⇒ **Nonlinear hierarchical models**
(analogous to models for radial sap flow profiles)

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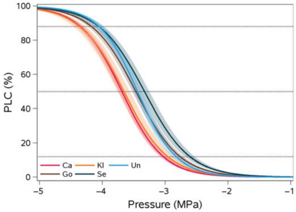

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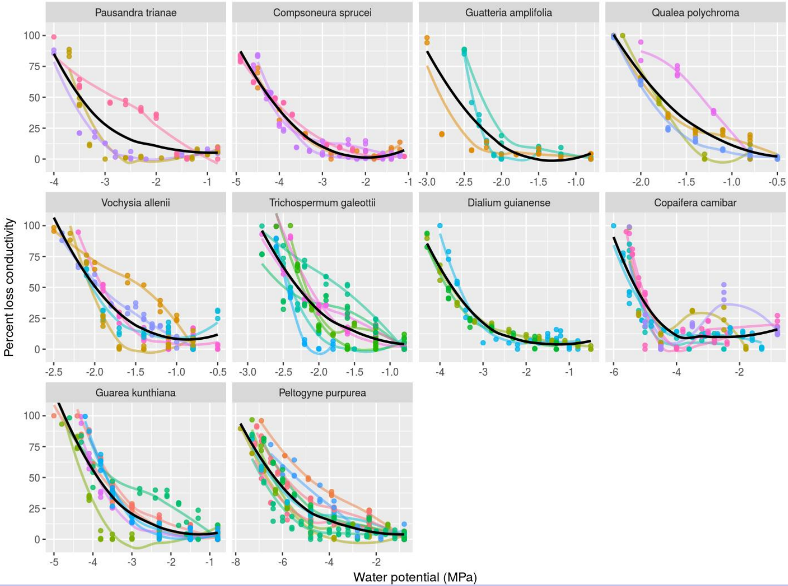
(analogous to models for radial sap flow profiles)

⇒ **Data analysis in progress**

Image source: Schuldt et al., 2016

Observed vulnerability curves



Third chapter: moving on to the big picture

- Do structural, functional and wood anatomical traits explain changes in productivity and hydraulic traits observed along the rainfall gradient?
- How are they related to non-structural carbohydrate storage?

Synthesizing the results of the gradient study

Variables that are relevant for the synthesis

- Tree size (tree height + diameter at breast height)
- Wood density
- Wood anatomy (average vessel diameter, vessel density, potential hydraulic conductivity)
- Wood non-structural carbohydrate contents
- Productivity (basal area increment/aboveground biomass increment)
- Climate information (?)

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- Climate information (?)
- **Sap flow data and vulnerability curves: unfortunately not available for all sites**

Research questions & hypotheses

Hypotheses from the project proposal related to these variables

- **Productivity**
  - increases with potential hydraulic conductivity
  - is related to tree height
  - is related to wood density (only at seasonally dry sites)
- **Potential hydraulic conductivity**
  - increases with tree height
- **Average vessel diameter**
  - increases with tree height
- **NSC storage**
  - increases with tree size
  - is higher at seasonally dry sites
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Data analysis

- Large amount of interrelated causal hypotheses about relationships between variables

⇒ Instead of focusing on the bivariate relationships in our system one at a time, test them all at once

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⇒ **Structural equation modeling**

- Modeling framework for the multivariate analysis of networks of causal hypotheses
- Allows to test whether a system significantly deviates from a model based on a-priori hypotheses about the system
- Modeling likely with R package `lavaan` or `piecewiseSEM`

Data analysis

- Dataset is not complete (NSC data are being measured)
- To show what the analysis will look like - results from a study using an analogous model:

  Kotowska, M.M., Röll, A., Link, R.M., Hertel, D., Hölscher, D., Leuschner, C., Waite, P.A., Moser, G., Toja, A., Schuldt, B. (2018): *Tree size in combination with wood anatomy determines whole-tree water use and productivity in the tropics* (in preparation)

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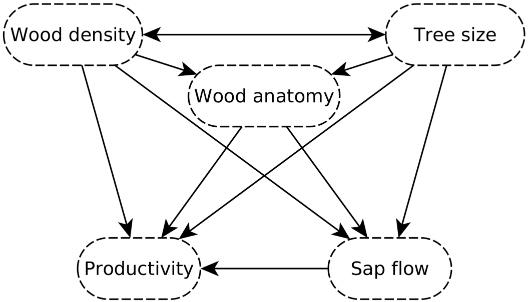
Meta-model



- **Meta-model:** relationships between theoretical entities/constructs of interest
- Updated because to reflect the different effects of the components of both tree size and sap flow

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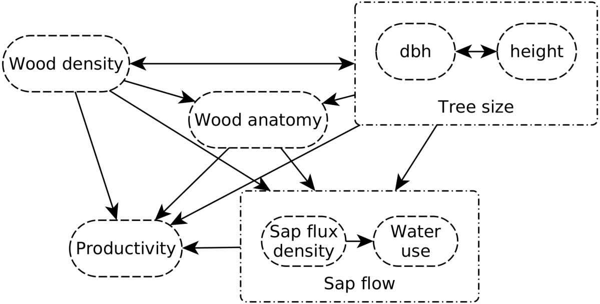

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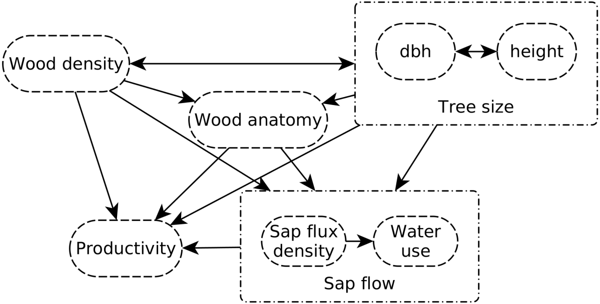

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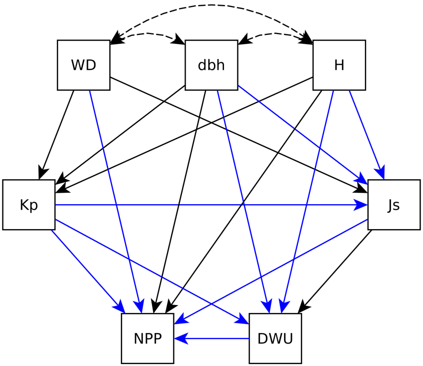
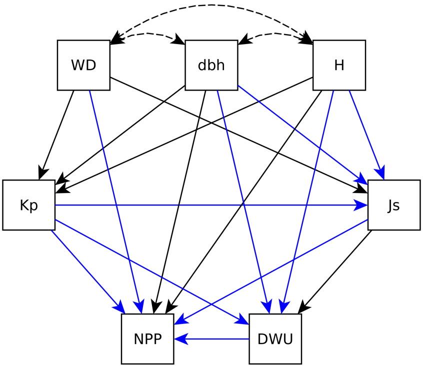
- For our model: remove sap flow component, add component for NSC

Causal diagram



- **Causal diagram:** Representation of the variables in the model and the assumed causal links
- Blue arrows: links related to a priori hypotheses

Causal diagram



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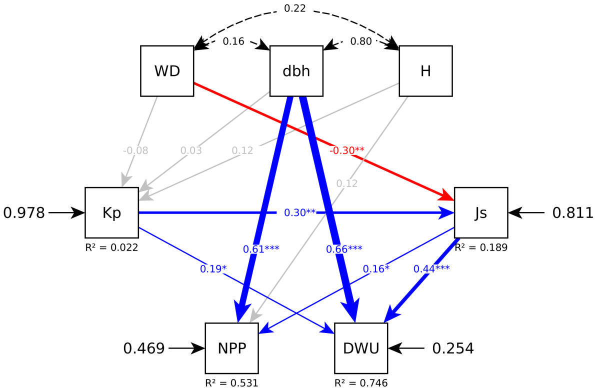
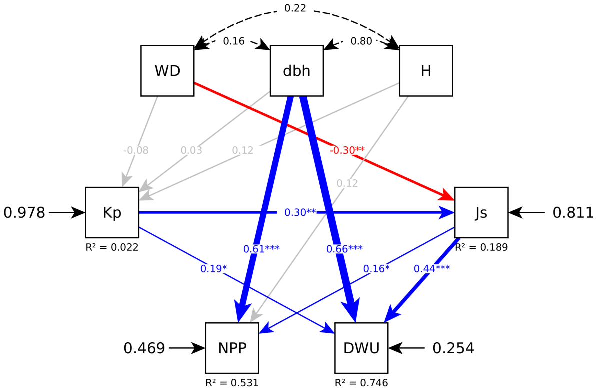
Path diagram of final model



- $\chi^2 = 3.35$, df $= 7$, p $= 0.850$; CFI $= 1.00$, RMSEA $= 0.00$
- Links were removed when related to tests of a priori hypotheses that were not significant

Path diagram of final model



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  - Dataset complete
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  - **Current state: data analysis**
- **Chapter 2: Vulnerability curves**
  - Leaf nutrient contents, branch NSC and branch anatomy missing
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Slides and source code of this presentation:

`https://github.com/r-link/2018-01-25_Presentation_PhD`


Thank you

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