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

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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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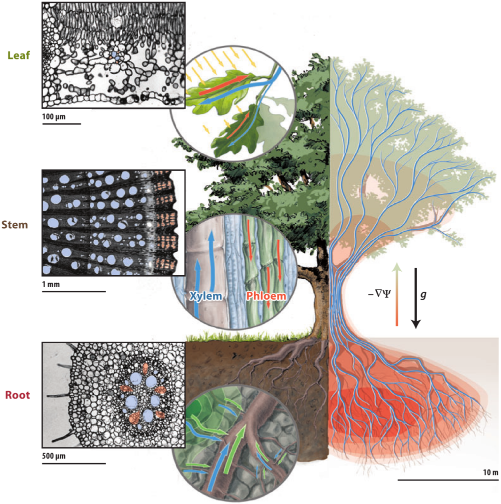
Water transport in plants



- 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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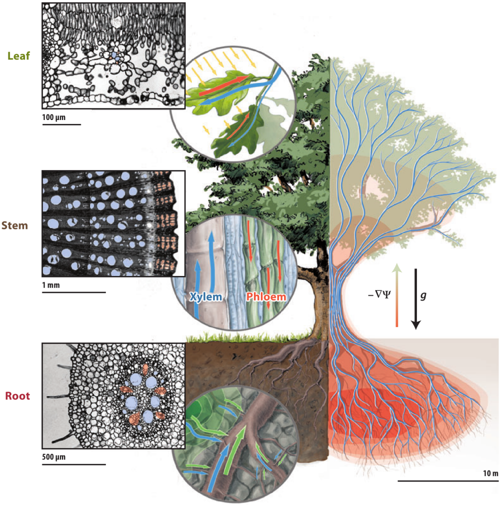

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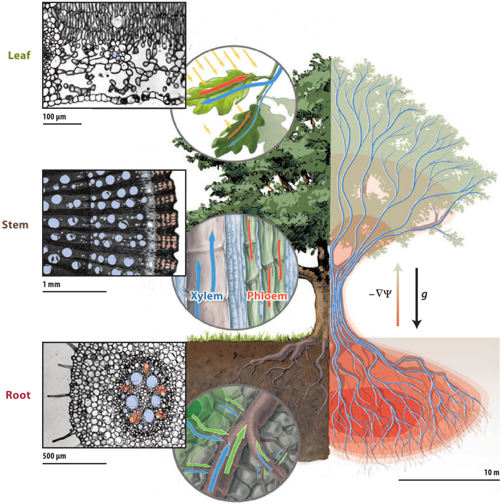

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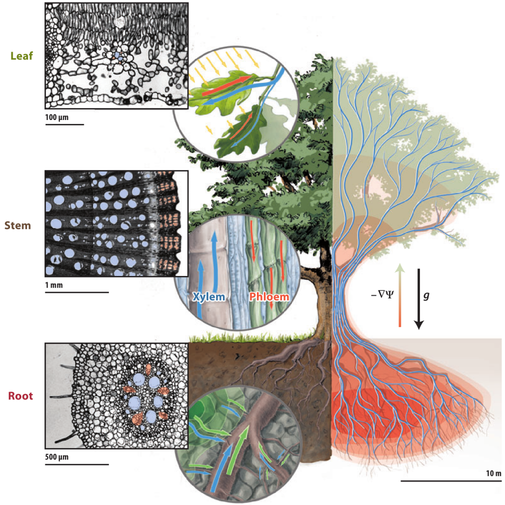

- Driving force: gradient in water potentials
- Continuous water columns held together by *cohesion-tension-mechanism*

→ 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
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- 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
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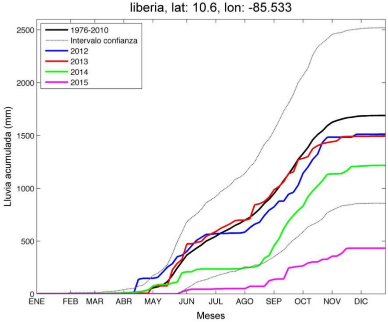

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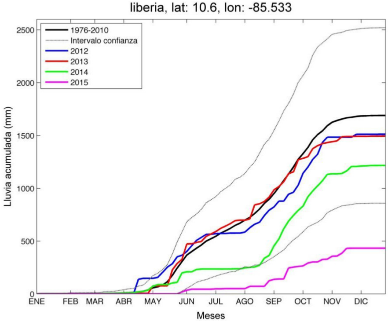

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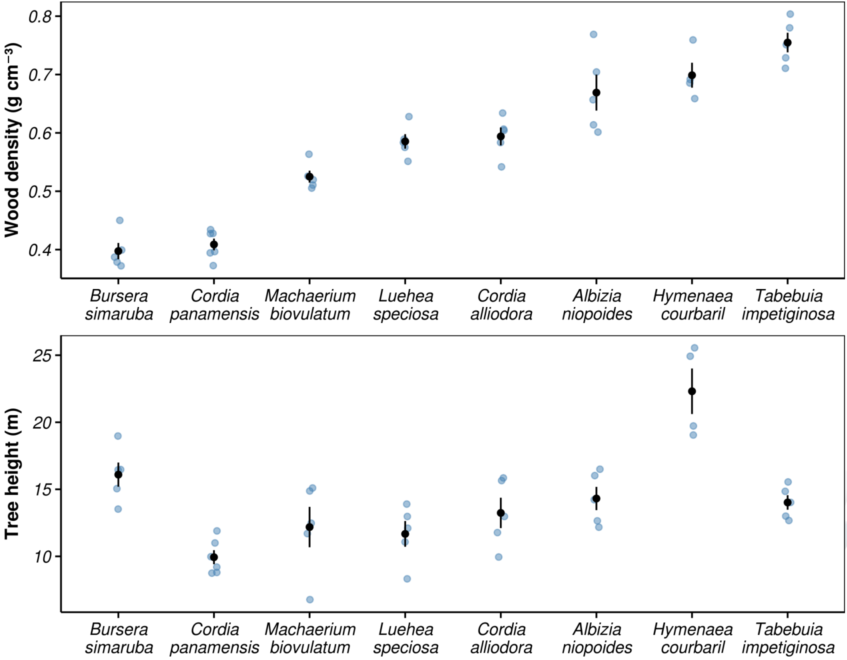
Wood density (g cm^{-3})
0.8
0.7
0.6
0.5
0.4
Bursera simaruba
Cordia panamensis
Machaerium biovulatum
Luehea speciosa
Cordia alliodora
Albizia niopoides
Hymenaea courbaril
Tabebuia impetiginosa
Tree height (m)
25
20
15
10
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First chapter: radial sap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

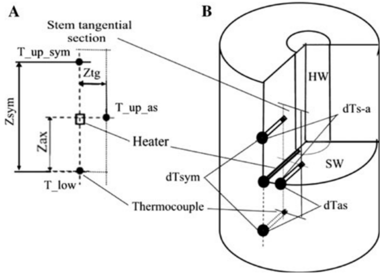
Additionally measured:

- 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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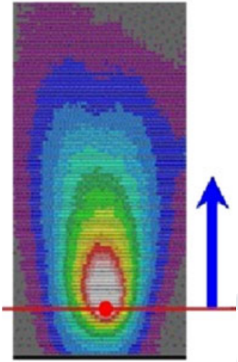

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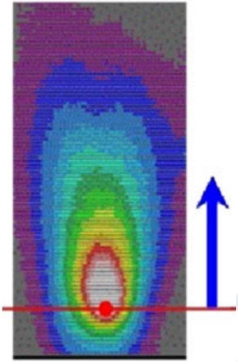

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Heat field deformation sensors

- 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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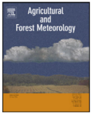

Short communication

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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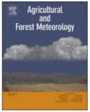

Calibration and comparison of thermal dissipation, heat ratio and heat field deformation sap flow probes for diffuse-porous trees

CrossMark

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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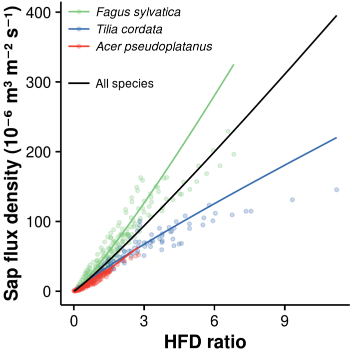

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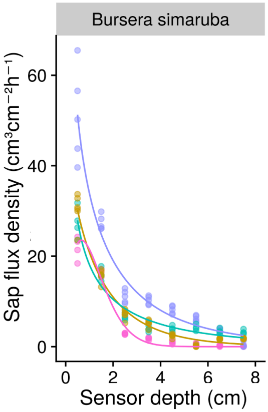
⇒ **Decision for analysis: better to put focus on radial gradients of sap flux**

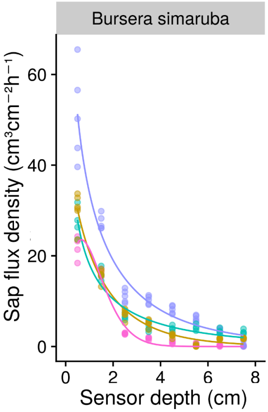
Research questions & hypotheses



- 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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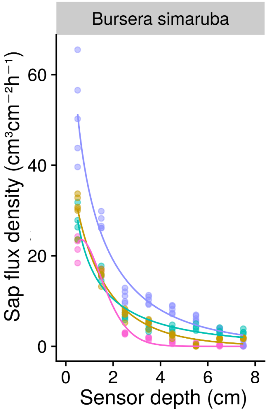

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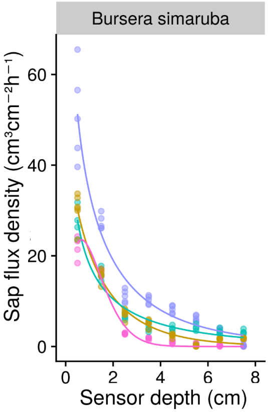

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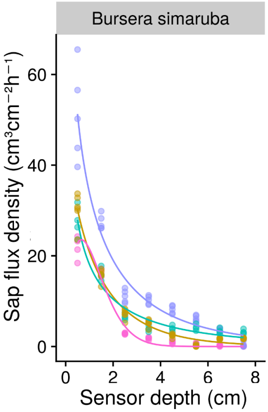

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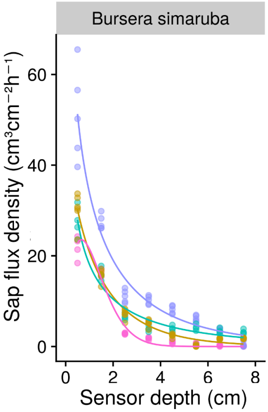

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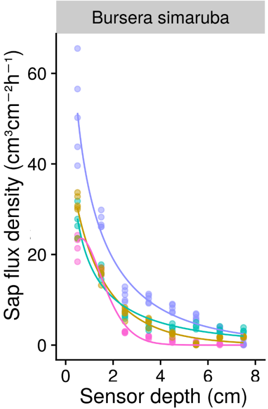
⇒ **Hypothesis:** The shape of radial sap flow profiles depends on **wood density** and **tree height**

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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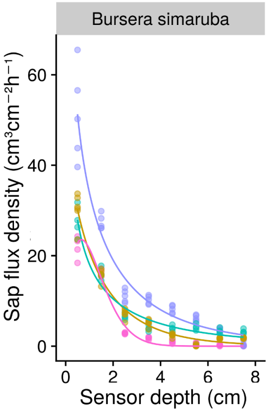

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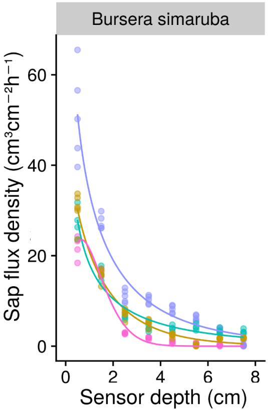

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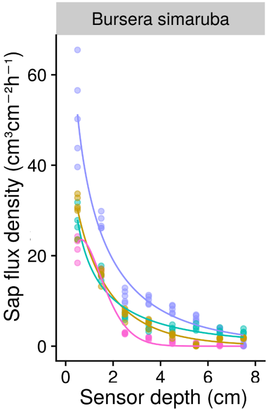

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- Analysis based on **Bayesian nonlinear hierarchical models**
  - **First stage of the model:** Nonlinear relationship between sensor depth and predicted flux density modeled with the density function of the Weibull distribution
  - **Second stage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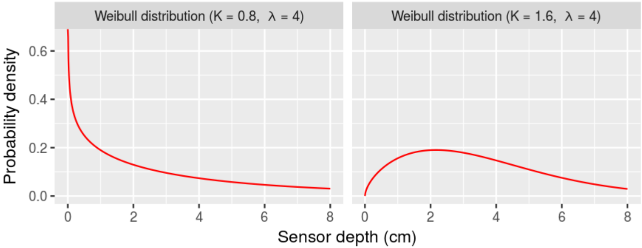

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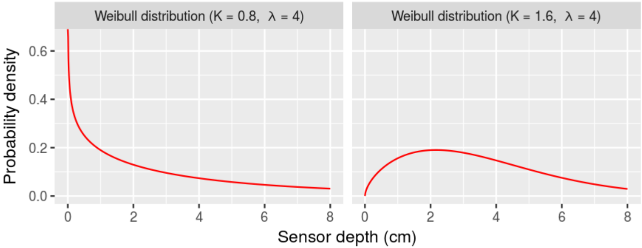

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  - Model fitting with the **Stan modeling language**
- Models still need tuning → shown results are from preliminary model based on R package `nlme`

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

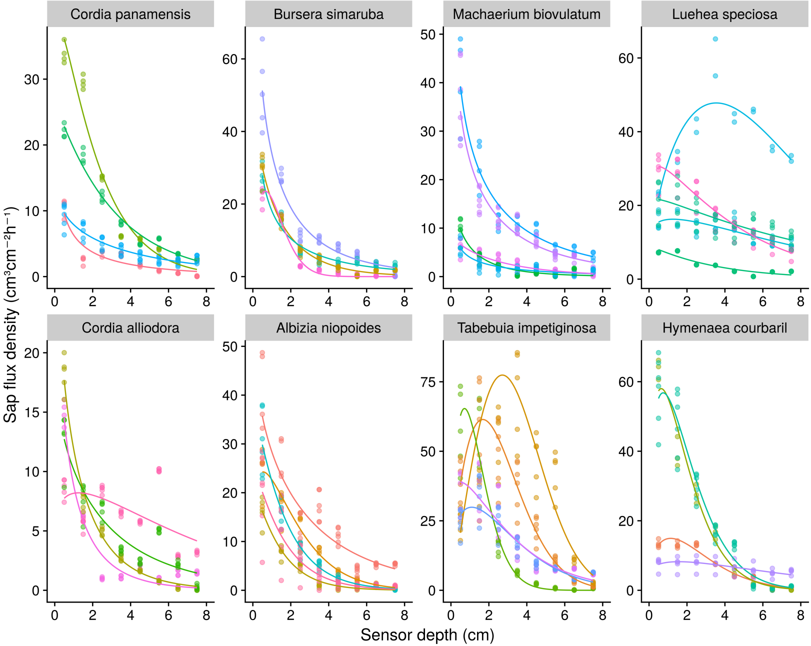
- $\lambda_{jk} = \exp(\beta_{\lambda 0} + \beta_{\lambda 1} \cdot WD + \beta_{\lambda 2} \cdot H + \beta_{\lambda 3} \cdot WD \cdot H + \epsilon_{j_\lambda} + \epsilon_{k_\lambda})$
- $K_{jk} = \exp(\beta_{K0} + \beta_{K1} \cdot WD + \beta_{K2} \cdot H + \beta_{K3} \cdot WD \cdot H + \epsilon_{j_K}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

Random effects

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

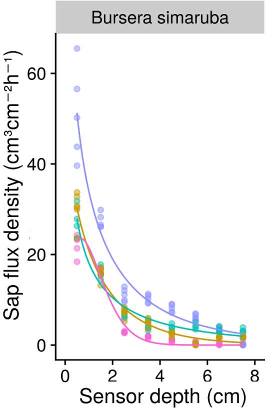
Variance covariates

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


Cordia panamensis
Bursera simaruba
Machaerium biovulatum
Luehea speciosa
Cordia alliodora
Albizia niopoides
Tabebuia impetiginosa
Hymenaea courbaril
Sap flux density ($cm^3 cm^{-2} h^{-1}$)
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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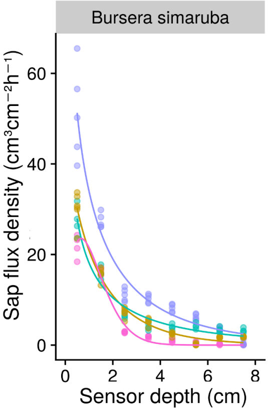
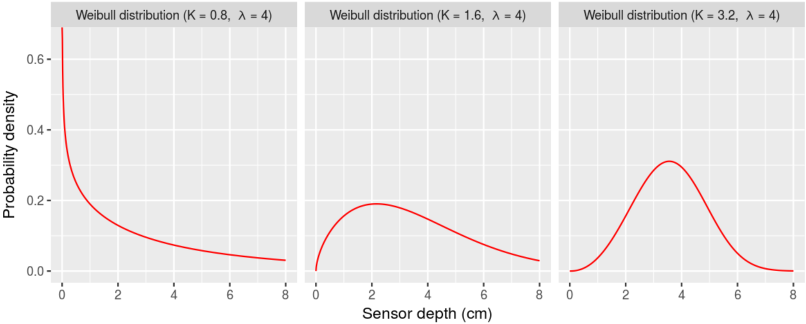
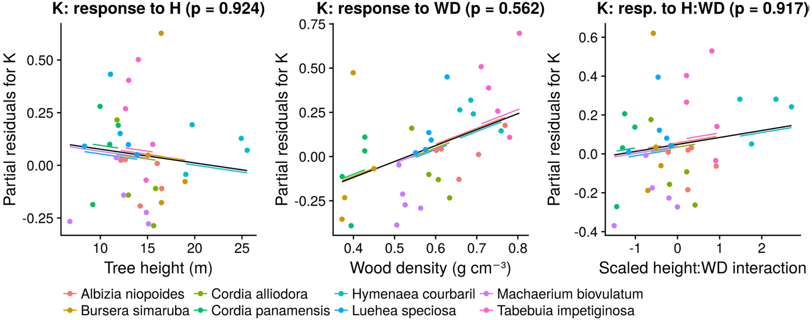


Preliminary results II - parameter model for K



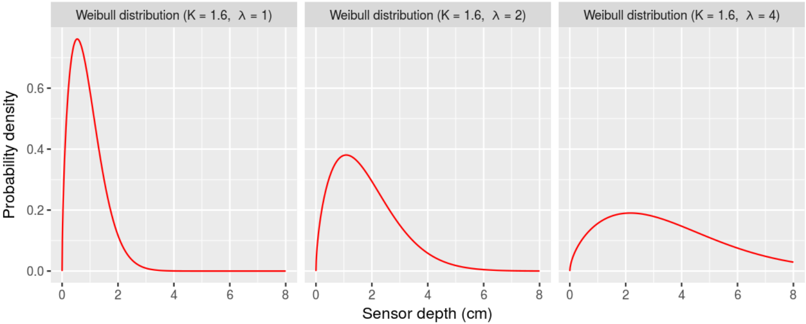
- **Weibull shape parameter K**

Preliminary results II - parameter model for K



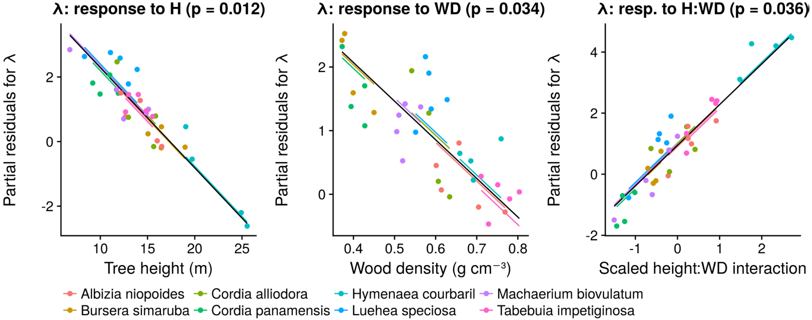
- **Weibull shape parameter K**
  - No significant height- and wood density effects

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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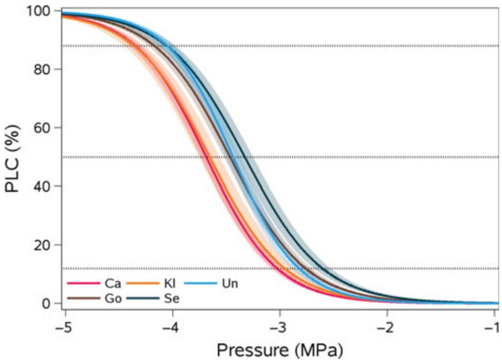
Second chapter: vulnerability curves

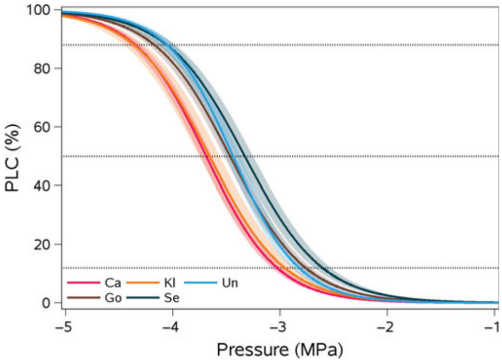


- Vulnerability curves: relationship between water potential and percentage loss of conductivity (PLC)

→ 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)

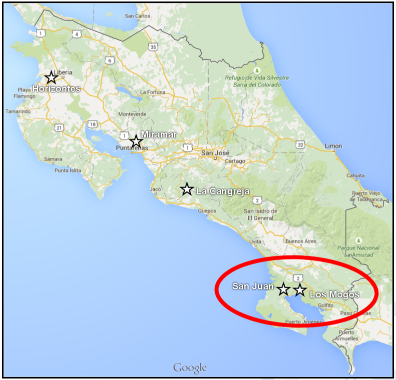


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Foto: http://sylvain-delzon.com/caviplace/

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Second chapter: vulnerability curves

Additionally measured for each tree:

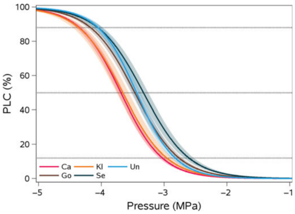
- Maximum vessel length (1 per tree)
- Leaf nutrient contents (1 per sample)
- Specific leaf area (1 per sample)
- Anatomy of branch wood (2 per sample)
- Huber value (1 per sample)
- Branch non-structural carbohydrate storage (1 per tree)

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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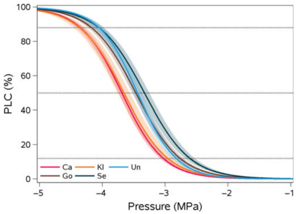

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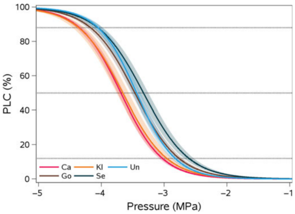

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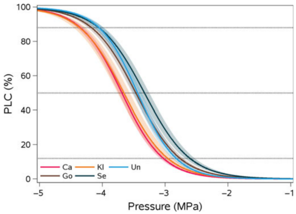

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⇒ **Nonlinear hierarchical models**
(analogous to models for radial sap flow profiles)

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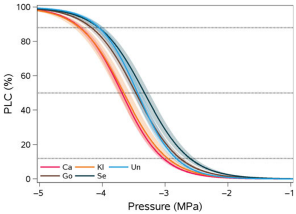

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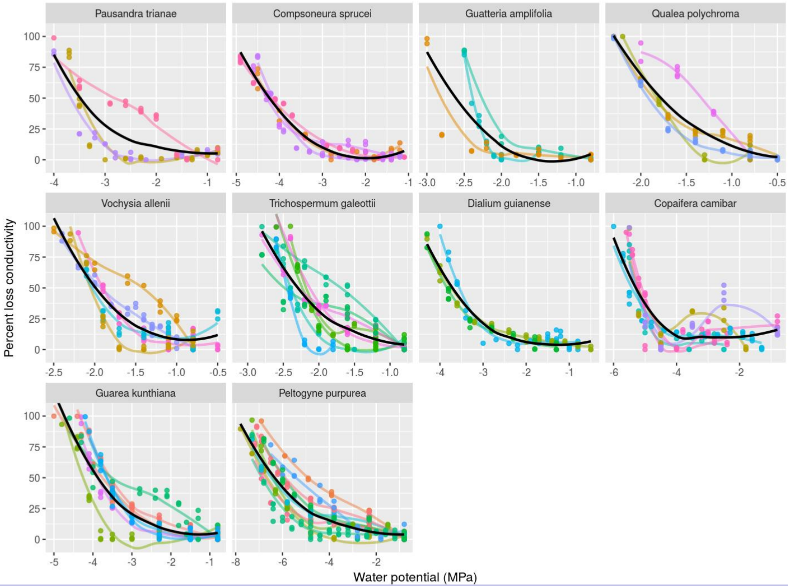
⇒ **Data analysis in progress**

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
  - is higher in deciduous trees/trees with isohydric drought response

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- 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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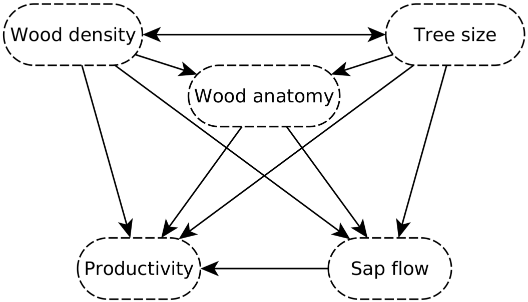
Meta-model



- **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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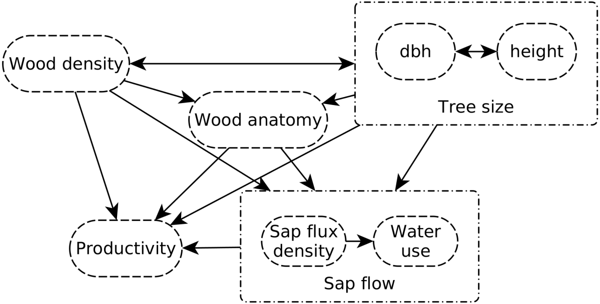

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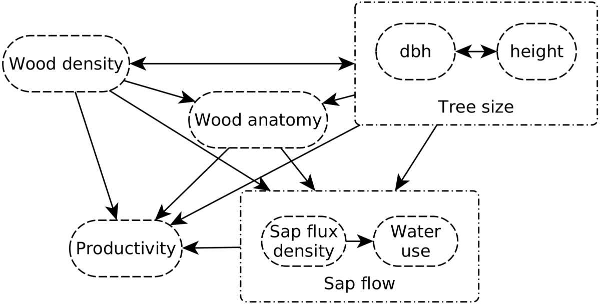

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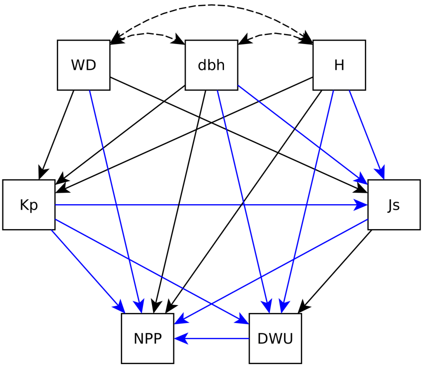
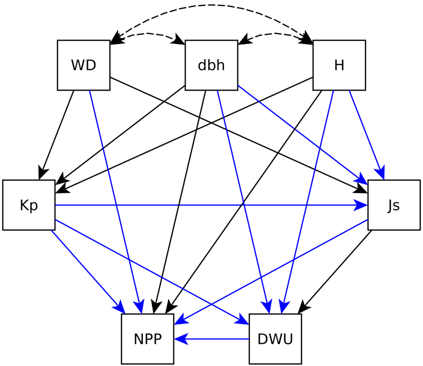
- Updated because to reflect the different effects of the components of both tree size and sap flow
- For our model: remove sap flow component, add component for NSC

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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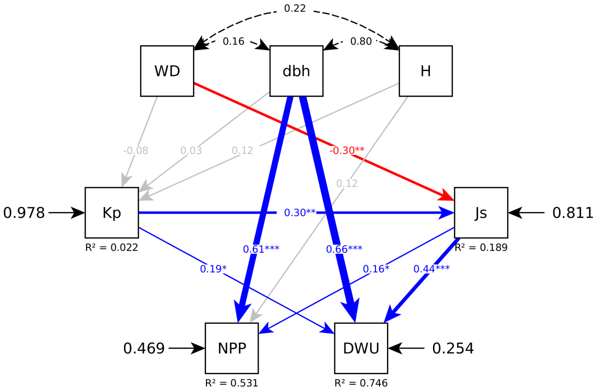
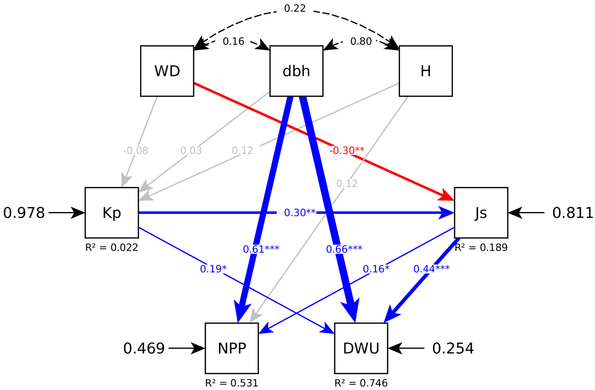
Path diagram of final model



- $\chi^2 = 3.35$, 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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Thanks list (in mostly alphabetical order):

Dagoberto Arias, Marvin Castillo, Sylvain Delzon, Moritz Doll, Adrian Fröhlich, Sebastian Fuchs, Steven Jansen, Christoph Leuschner, Erick Naranjo, Maynor Rodriguez, Luis Guillermo Romero, Bernhard Schuldt, Katja Steinhoff, Juan Carlos Valverde, the CIPA staff, the EEFH staff, the Escuela de Ingiería Forestal of the TEC, and everyone who feels forgotten


Thank you

References

- **Carpenter, B, Gelman, A, Hoffman, MD, Lee, D, Goodrich, B, Betancourt, M, Brubaker, M, Guo, J, Li, P, Riddell, A, 2017.** Stan: A probabilistic programming language. *Journal of Statistical Software* **76(1)**. https://doi.org/10.18637/jss.v076.i01.
- **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.
- **Lefcheck, JS, 2015.** piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution* **7(5)**, 573-579. https://doi.org/10.1111/2041-210X.12512.
- **Nadezhdina, N, Vandegehuchte, MW, Steppe, K, 2012.** Sap flux density measurements based on the heat field deformation method. *Trees* **26(5)**, 1439-1448.
- **Pinheiro, J, Bates, D, DebRoy, S, Sarkar, D, R Core Team, 2017.** nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131. https://CRAN.R-project.org/package=nlme.
- **Rosseel, Y, 2012.** lavaan: An R Package for Structural Equation Modeling. *Journal of Statistical Software* **48(2)**, 1-36. http://www.jstatsoft.org/v48/i02/.
- **Schuldt B, Knutzen F, Delzon S, Jansen S, Müller-Haubold H, Burlett R, Clough, Y, Leuschner, C, 2016.** How adaptable is the hydraulic system of European beech in the face of climate change-related precipitation reduction?. *New Phytologist* **210(2)**, 443-458.
- **Stroock, AD, Pagay, VV, Zwieniecki, MA, Holbrook, MN, 2014.** The physicochemical hydrodynamics of vascular plants. *Annual Review of Fluid Mechanics* **46**, 615–642.
- **Vandegehuchte, MW, Steppe, K, 2012.** Interpreting the Heat Field Deformation method: Erroneous use of thermal diffusivity and improved correlation between temperature ratio and sap flux density. *Agricultural and Forest Meteorology* **162**, 91-97.